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Review article

Anticlockwise or clockwise? A dynamic *Perception-Action-Laterality* model for directionality bias in visuospatial functioning

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ABSTRACT

Orientation bias and directionality bias are two fundamental functional characteristics of the visual system. Reviewing the relevant literature in visual psychophysics and visual neuroscience we propose here a three-stage model of directionality bias in visuospatial functioning. We call this model the '*Perception-Action-Laterality*' (PAL) hypothesis. We analyzed the research findings for a wide range of visuospatial tasks, showing that there are two major directionality trends in perceptual preference: *clockwise versus anticlockwise*. It appears these preferences are combinatorial, such that a majority of people fall in the first category demonstrating a preference for stimuli/objects arranged from left-to-right rather than from right-to-left, while people in the second category show an opposite trend. These perceptual biases can guide sensorimotor integration and action, creating two corresponding turner groups in the population. In support of PAL, we propose another model explaining the origins of the biases – how the neurogenetic factors and the cultural factors interact in a biased competition framework to determine the direction and extent of biases. This dynamic model can explain not only the two major categories of biases in terms of direction and strength, but also the unbiased, unreliably biased or mildly biased cases in visuosptial functioning.

Contents

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1. Introduction

Everyday we experience and interact with a variety of objects, pictures and many spatial configurations in two or three dimensions. One peculiarity of our experience is the sensitivity to orientation even though we are not usually aware of this fact in daily activities. This aspect of our visual functioning, however, has a long history of empirical investigation in visual psychophysics and visual neuroscience in both humans and model organisms. Researchers in these two areas have shown that stimuli oriented cardinally are perceived more precisely than those oriented obliquely. Thus our performances in contrast sensitivity (Campbell and Kulikowski, 1966; Mitchell et al., 1967), stereoacuity (Mustillo et al., 1988), grating acuity (Berkley et al., 1975; Campbell et al., 1966; Furmanski and Engel, 2000), and vernier acuity (Corwin et al., 1977; Saarinen and Levi, 1995; Westheimer and Beard, 1998) are better at the cardinal than oblique orientation. One hypothesis is that this sort of asymmetry, often termed as the oblique effect (Appelle, 1972), occurs because more V1 (primary visual/striate cortex) cells are devoted to the cardinal than oblique orientations (Furmanski and Engel, 2000; Li et al., 2003).

In addition to the oblique effect, research has demonstrated some other types of orientation asymmetry, particularly in visual search. For example, visual search is more efficient when the target element is presented at an oblique orientation with horizontally or vertically oriented distarctors than when these orientations are interchanged (Foster et al., 2000; Foster and Ward, 1991; Foster and Westland, 1995; Westland and Foster, 1995). Wolfe et al., (1992) demonstrated that visual search benefits if the target and distractors are sufficiently different in orientation; the search is easier if the target is the sole steep line-element (-10° from vertical) and the distractors are all shallow line-elements ($\pm 50^\circ$ from vertical). A similar advantage was reported when the target was uniquely tilted either left or right relative to distractors. Homogeneity of distractor orientation is another important candidate in visual search. Visual search is efficient if target-distractor differences are greater than about 10–15° in a background field of homogeneously oriented distractors (Foster and Westland, 1995; Wolfe et al., 1999). It is easy to find a vertical target among homogeneous distractors tilted either left or right than a target among heterogeneous distractors tilted left and right (Wolfe and Horowitz, 2004). Thus it has been suggested that orientation stimuli are coded categorically using the dimensions like steep, shallow, left-tilted and right-tilted (Wolfe et al., 1992; Wolfe and Horowitz, 2004). When distractors are heterogeneously oriented this categorization deteriorates, and visual search becomes very inefficient, requiring the deployment of attention from line to line at random (Wolfe et al., 1999). This has been further supported in other empirical studies. For example, Proulx and Egeth (2006) presented a vertical line as the target on a display of 2–8 distractors tilted clockwise or counterclockwise ($\pm 15^\circ$ to $\pm 35^\circ$ from vertical), and demonstrated that the average time required for finding a target increases not only with the number of distractors, but also with increasing orientation similarity between the target and distractors. Other studies showed that the average response time for visual search was longer when the uniquely oriented target line (right-tilted or vertical) was absent rather than present on a display of heterogeneously oriented distractors (tilted left and right; Proulx, 2010; Proulx and Egeth, 2008), but it was shorter on a display of homogeneously oriented distractors (tilted left; Proulx, 2010). This suggests that the advantage of a target absence is due to ease of perceptual processing, such as grouping by similarity of texture, in a background field of homogeneously oriented distractors (Duncan and Humphreys, 1989).

Another type of orientation effect has been demonstrated in both visual search and shape discrimination tasks, such as humans tend to perform best in visual search and 3D shape discrimination tasks under top-left lighting conditions (Elias and Robinson, 2005; Gerardin et al., 2007; Mamassian et al., 2003; Sun and Perona, 1998; Thomas et al., 2010). Sun and Perona (1998), for example, were the first to demonstrate that shaded targets are detected more quickly when the illumination position is between 30° and 60° to the left of vertical. As they claimed, both left- and right-handed observers showed this tendency, but it was more pronounced among the right-handers. However, in agreement with subsequent studies (Mamassian and Goutcher, 2001; McManus et al., 2004), a recent study failed to associate this orientation effect with handedness; instead, it demonstrated that cultural factors, such as scanning habits, can affect the way visual scenes are inspected and organized in determining the assumed light source direction (Andrews et al., 2013). Perhaps, as Proulx (2014) has precisely suggested, the perception of shape from shading may not be always necessarily based on a hard-wired internal representation of lighting direction; rather, it assesses the direction of lighting in the scene adaptively. Thus the handedness effect most likely arises from the experience one has with an environment, and suggests that a form of lateralized function, like handedness, interacts with orientation related processing.

Related to the top-left lighting preference is the observation of a spontaneous preference for face-like stimuli shown by both human newborns (Goren et al., 1975; Johnson, 2005), and domestic chicks (Salva et al., 2012). Research using face and face-like stimuli has shown that this kind of preference abolishes as a result of inversion of contrast polarity in human newborns (Farroni et al., 2005) and domestic chicks as well (Salva et al., 2012). It has been argued that a stimulus is perceived as face-like only if it appears with the correct luminance, similar to a face under (natural) top-lit illumination (Farroni et al., 2005; Salva et al., 2012), and that the right hemisphere might play a crucial role in this kind of social orienting responses (Salva et al., 2012). We propose that perhaps this is due to a social orienting bias in perception: portraits, photographs, and advertisements are normally lit from the left rather than from the right (McManus et al., 2004; Thomas et al., 2008), and artists prefer to locate the light at an angle left of the vertical when illuminating paintings (McDine et al., 2011), which in turn can create a more favorable purchase intention in customers (Hutchison et al., 2011). Orientation perception does not influence only information processing efficiency and social orienting responses, but the aesthetic preference for a particular arrangement of stimuli or pictures as well. People usually prefer pictorial arrangements that possess left-to-right directional cues over their mirror reversed pictures; and this preference can be associated with handedness (Freimuth and Wapner, 1979; McLaughlin et al., 1983; Mead and McLaughlin,

1992) and cultural factors, such as reading/writing habits (Chokron and De Agostini, 2000; Friedrich and Elias, 2016). In addition to such a horizontal directionality bias in aesthetic judgment of visual arts, further evidence indicates that left-to-right directional preference or bias might also occur in other visuospatial tasks, such as line bisection (Bowers and Heilman, 1980; for a metaanalytic review, see Jewell and McCourt, 2000) and vernier offset detection (Karim and Kojima, 2010a,b). On the other hand, the most widely known behavioral lateralization is the earliest demonstration that humans prefer to turn rightward rather than leftward (Blumenthal, 1928; Brigden, 1935; Gesell, 1938; Gesell and Ames, 1950; Lund, 1930; Szymanski, 1913; Turkewitz et al., 1965a,b), although some contradictory findings have emerged in other studies (Mohr and Bracha, 2004; Mohr et al., 2004, 2003; Toussaint and Fagard, 2008). However, the current theoretical notion of the left-right asymmetry places particular emphasis on the horizontal stimulus orientation, and cannot explain perceptual anisotropies (directional dependence) in the cardinal and oblique axes in a generalized fashion. Secondly, although many studies have reported the existence of both perceptual and motor lateralization in humans and non-human animals, there is no theory that can establish a link between visual perceptual bias and turning tendency in these species. Thus our current knowledge remains insufficient to explain perceptual anisotropies across the stimulus orientations, as it is unclear how such anisotropies guide motor responses.

In this review, we attempt to develop for the first time a mechanistic account of such anisotropies, develop a spatial-mapping model, and establish a link between the directionality bias in visuospatial perception and turning tendency, combining evidences from a wide variety of visuospatial tasks, such as picture aesthetic judgment, line alignment judgment, space mapping or spatial coding, and turning or rotating behaviors exhibited in different situations. Furthermore, we also propose another dynamic model for the origins of the perceptual and behavioral anisotropies - how the neurobilogical or neurogenetic factors and environmental or cultural factors interact to determine the direction and extent of the biases. This will advance our understanding of perceptual and functional (action) laterality of the brain.

2. Directionality bias in aesthetic judgment of pictures or objects

Humans prefer some shapes of objects or pictures to others, and this aesthetic judgment occurs even in the absence of any semantic or narrative association (Latto, 2005). Numerous studies have demonstrated that the asymmetry in aesthetic judgment is related to handedness of the observers. For example, studies employing mirror image pairs of landscape photographs and paintings showed that right-handers prefer pictorial arrangements possessing left-to-right directionality or that contain the region of greatest weight or interest on the right side (e.g., Beaumont, 1985; Freimuth and Wapner, 1979; Levy, 1976; Mead and McLaughlin, 1992). On the contrary, left-handers typically exhibit preferences for patterns having right-to-left directionality or for those that contain the region of greatest weight or interest on the left side (e.g., Banich et al., 1989; Christman and Dietsch, 1995; Levy, 1976; Mead and McLaughlin, 1992). These findings can be interpreted as reflecting an influence of hemispheric asymmetry between the left- and right-handers. As the left- and right-handers exhibit different degrees of hemispheric asymmetry, they in turn exhibit different preferences for asymmetric stimuli. Two specific and opposing theoretical interpretations of these facts have been derived from the works of Levy (1976), and Freimuth and Wapner (1979). First, Levy's (1976) study on aesthetic judgment reported that asymmetric pictures judged to have centers of interest to the right of the center were preferred over their mirror reversed versions, the effect being true for dextrals (right-handers), but not for sinistrals (left-handers). Levy explained her findings by the hemispheric activation model which suggests that differential activation of a hemisphere produced an attentional orientation bias to the contralateral visual field (cf. Kinsbourne, 1970, 1974). Assuming that the right hemisphere is more activated than the left hemisphere when a dextral is engaged in visuospatial task, she argued that such an attentional bias to the left visual field would make a symmetrical picture look unbalanced. If, on the other hand, a picture were asymmetric in the direction opposite to the attentional bias, the net perceptual result would be a state of balance and the aesthetic response would be positive. Pictures that have areas of greater interest or weight in their right halves are then preferred because those asymmetries counteract the asymmetry produced by attentional bias to the left visual field.

Freimuth and Wapner (1979), in contrast, reported that dextral subjects preferred paintings with left-to-right directional properties. According to them, directional cues that suggest a left-to-right sequence may draw attention to the rightward portions of the picture, but unlike Levy's view such an attentional draw need not necessarily create the perceptual balance. Freimuth and Wapner's findings were later supported in a few studies (e.g., McLaughlin et al., 1983; Mead and McLaughlin, 1992). For example, McLaughlin et al. (1983) demonstrated that dextral subjects preferred asymmetric paintings that contained a rightward position of the area of major interest and that sinistrals behaved in an exactly opposite fashion. Mead and McLaughlin (1992) examined the effects of directionality, interest and weight, using four painting types: (i) paintings with asymmetry of directionality only; (ii) paintings with asymmetry of weight only; (iii) paintings with asymmetry of interest only; and (iv) paintings that were discordant for the dimensions of directionality and weight (i.e., with left-to-right directionality and left-biased weight or with right-to-left directionality and right-biased weight). Subjects would give a score of +1 for choosing a painting with left-to-right directionality or with greater weight or interest in the right half. The sum of these values was defined as the R (right) score. A score of −1 was given for choosing a painting with right-to-left directionality or with greater weight or interest in the left half. The sum of these values was defined as the L (left) score. Mead and McLaughlin (1992) calculated difference scores (D) as ratios of the algebraic sum of L and R divided by the sum of the absolute values of L and R. Thus, a positive value of D indicates the preference for a painting with left-to-right directionality or for a painting with greater weight or interest on the right. For the directional cues (Dir) versus asymmetry of weight (Wt) paintings in which directional cues suggested motion away from the areas of greater weight, choices of the paintings with left-to-right directionality and left-based weight were scored +1, and their sum was the R score. In contrast, choices of the paintings with right-to-left directionality and right-based weight were scored −1, and their sum was the L score. Their data are shown in Table 1. The figures in this table indicate that dextrals and inverted sinistrals preferred paintings containing left-to-right directional cues over their mirror-reversed pictures, and also paintings with greater weight on the left portions of the picture space; no preferences were found for paintings with discordant weight and direction or for paintings with asymmetrically located elements of interest.

The results of Freimuth and Wapner (1979) and Mead and McLaughlin (1992) have been replicated in latter studies. For example, Christman and Pinger (1997) conducted a series of experiments with right-handed subjects. Subjects were presented with the mirror-image pairs of geometric objects or facing objects (as shown in Fig. 1) located one above the other in random order, and asked to indicate which object was more aesthetically pleasing or interesting to look at; if subjects felt that the two objects

Table 1
Mean with SE of aesthetic preference scores (Ds).

Participant group	Painting type			
	Dir	Wt	Int	Dir vs Wt
	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)
Dextrals	0.137 (.030)	−0.056 (.025)	0.053 (.077)	0.065 (.046)
Sinstrals	0.205 (.037)	−0.070 (.026)	0.045 (.063)	0.112 (.055)
Inverted subjects	0.294 (.034)	−0.090 (.030)	0.081 (.080)	0.183 (.062)
Non-inverted subjects	0.024 (.075)	−0.030 (.049)	−0.030 (.127)	−0.034 (.101)

Source: Mead and McLaughlin, 1992.
Note. Dir- Directional cues, Wt- Asymmetry of weight, Int- Asymmetry of interest.

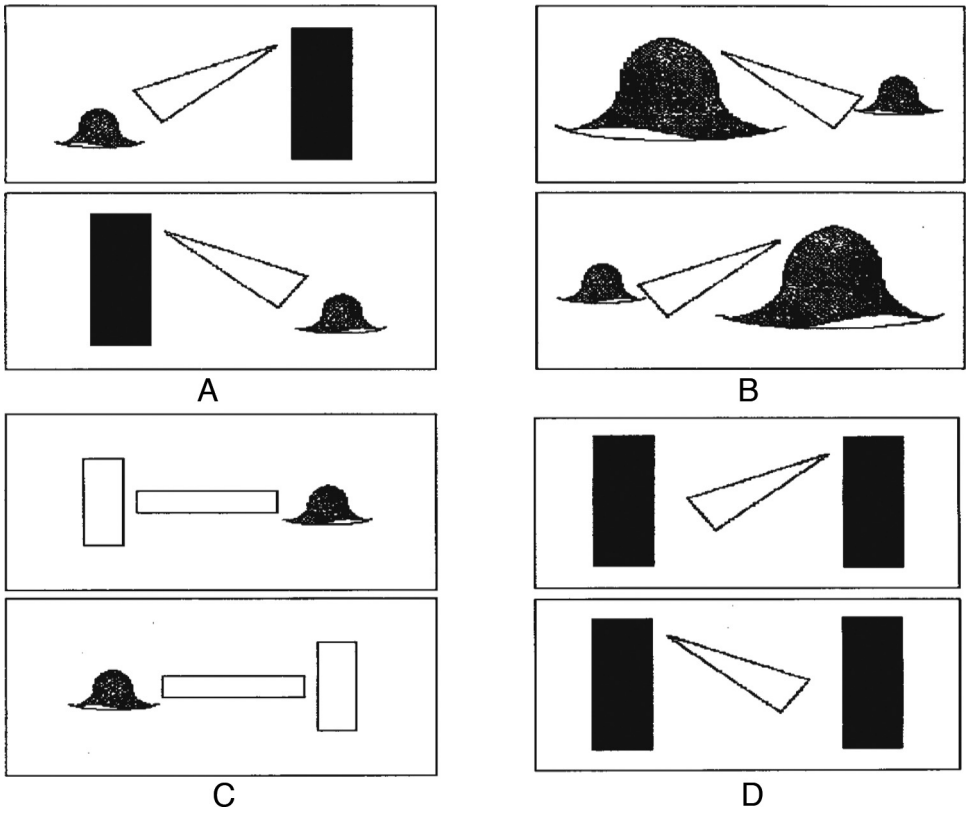

Fig. 1. Example stimuli used in aesthetic judgment experiment of Christman and Pinger, 1997. (A) Top: right-biased weight, left-biased interest, and left-to-right directionality, Bottom: left-biased weight, right-biased interest, and right-to-left directionality. (B) Top: left-biased weight, balanced interest, and right-to-left directionality, Bottom: right-biased weight, balanced interest, and left-to-right directionality. (C) Top: absent weight, right-biased interest, and absent directionality, Bottom: absent weight, left-biased interest, and absent directionality. (D) Top: balanced weight, absent interest, and left-to-right directionality, Bottom: balanced weight, absent interest, and right-to-left directionality (From Christman and Pinger, 1997; with permission).

were equivalent, they could respond 'no preference'. Their results showed that most subjects preferred the objects which contained left-to-right directionality; no object pairs lacking in directionality yielded significant preferences (Christman and Pinger, 1997). The preference for objects with left-to-right directionality was not dependent on the absolute positioning of the pictorial elements; rather, any object which was located to the left of a left-to-right directional cue yielded a significant preference. Thus directionality plays an important role in determining patterns of aesthetic preference: objects with asymmetries of weight and/or interest alone yielded no systematic preferences. In support of Christman and Pinger's (1997) finding, Palmer et al., (2008) found that people usually prefer the right-facing rather than left-facing objects or stimuli.

Research has also shown evidence of the influence of reading habits on the directionality bias in aesthetic perception. This has been evident in both naturalistically produced photographs studies and controlled laboratory experiments. For example, González (2012) compared portrait studio photographs taken by Iranian (right-to-left readers) and Spanish (left-to-right readers) photographers in the nineteenth century and demonstrated in line with the above aesthetic studies an overall preference for left-to-right directionality in photographs taken by Spanish photographers, in contrast to a preference for right-to-left photographs taken by Iranian photographers. In a controlled study, Nachson et al., (1999) examined aesthetic preferences in Russian (left-to-right), Hebrew (right-to-left) and Arabic (right-to-left) participants, presenting them pairs of pictures of human faces and bodies that turned either left or right. The Russian readers exhibited a significant preference for the right-facing pictures, and both the Hebrew and Arabic readers showed a preference for the left-facing pictures, the results being significant in the Hebrew but not in the Arabic readers. Chokron and De Agostini (2000) and Ishii et al., (2011) used very identical methods to examine aesthetic appreciation in participants of two cultures with opposite scanning habits. They demonstrated that left-to-right readers (French or Australian)

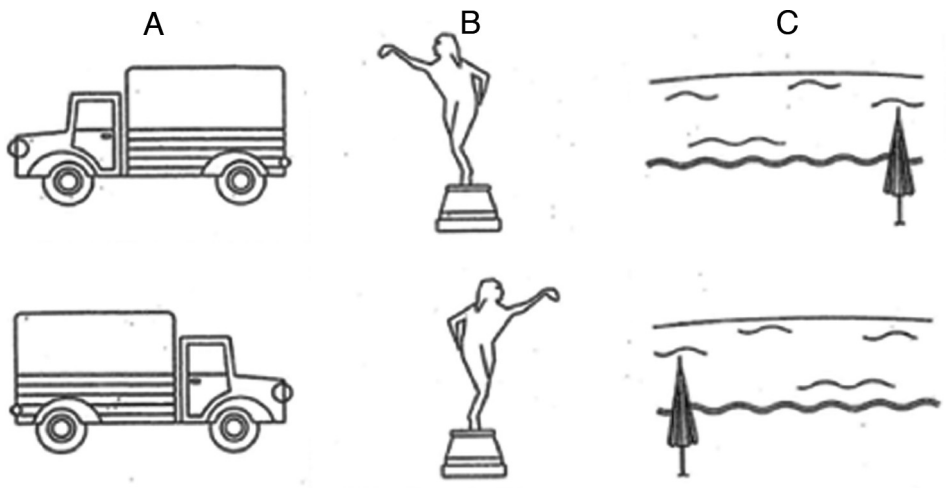

Fig. 2. Sample aesthetic preference items. Subjects were presented pictures from three categories: (A) pictures representing moving objects, (B) pictures representing static objects, and (C) pictures representing landscapes (From Chokron and De Agostini, 2000; with permission).

preferred static objects or mobile images that displayed a left-to-right directionality whereas right-to-left readers (e.g., Israeli or Japanese) preferred objects and images with a right-to-left directionality (Fig. 2). Though they did not find such differences when used pictures of landscapes as the stimuli a recent study demonstrated that the effect of scanning habits might be robust even on the aesthetic perception of the pictures of landscapes (Friedrich et al., 2014). In fact, this study examined the effect of scanning habits on aesthetic preference for both static and dynamic stimuli (images and videos of mobile objects and landscapes), and reported a significant leftward bias in the left-to-right readers, which was strongest for dynamic stimuli, but failed to identify a directional bias for static or dynamic images in the right-to-left readers. These findings have been corroborated by the findings of a most recent study conducted on native Hindi (left-to-right) and Urdu (right-to-left) readers (Friedrich and Elias, 2016). The association of reading or writing habits to directionality bias in aesthetic perception can be robust for action stimuli as for the dynamic stimuli. In support of this, one study has shown that participants of a culture with left-to-right writing direction, such as Italian, perceived the same athletic performance (a soccer goal) as stronger, faster, and more beautiful if presented with a left-to-right rather than right-to-left trajectory, and this trend was completely opposite in the participants of a culture with right-to-left writing direction, such as Arabic (Maass et al., 2007).

All the data above clearly suggest that the preference for a left-to-right directional cue reflects a stable, underlying directionality bias in perceptual processing of visual objects at horizontal orientation. However, what happens if the same objects/pictures are presented at vertical orientation or in a tilted fashion, say $\pm 45^{\circ}$ from horizontal (i.e., tilted clockwise or anticlockwise)? In such presentations the objects/pictures still possess the same directional cue (left-to-right or right-to-left), but does the preference for left-to-right directionality still exist? The existing knowledge of aesthetic judgment of pictures cannot answer these sorts of questions. However, the analysis below of the perceptual asymmetries in line alignment (symmetry) judgment can give a potential solution to this problem.

3. Directionality bias in line alignment (symmetry) judgment

As mentioned at the beginning of this paper, one of the most fundamental properties of our visual functioning is the orientation asymmetry. There is clear evidence of the cardinal superiority over the oblique orientation, and its neural basis (Furmanski and Engel, 2000; Li et al., 2003). In addition to the evidence of the orientation effect, some recent studies have demonstrated that our visuospatial performance can vary even within an orientation depending on spatial organization or layout of the stimuli (Fig. 3; Karim and Kojima, 2010a,b; for a review, see Karim and Kojima, 2010c). In one study, Karim and Kojima (2010a) found that observers were generally better at discriminating a vertical offset for a pair of horizontal light bars (vernier features) arranged side-by-side with a large gap between them if the right-hand bar was below the left-hand bar than vice versa (Fig. 3A,B; horizontal). Similarly, for a pair of vertically oriented light bars, one above the other, the horizontal offset detection was better if the lower bar was on the left of the upper bar rather than on its right (Fig. 3A,B; vertical). In another study, they have shown that this effect can be generalized to the oblique orientation (Karim and Kojima, 2010b; Fig. 3A,B; oblique). However, there were some individual differences, with a few observers showing an opposite trend as an exception to the overall findings in both these studies. Karim and Kojima (2010a,b) suggested that these findings can be associated with neuronal preference or with cerebral lateralization via handedness of the observers.

If the findings of Karim and Kojima (2010a) are compared to the findings about aesthetics of visual arts (see prior section) we see that there is a consistency between perceptual precision and aesthetic preference: what is oriented from left-to-right direction is more understandable and aesthetically more appealing than what is oriented from right-to-left direction, possibly due to the increased efficiency of information processing at that orientation. Though the stimuli that Karim and Kojima, used in their studies were different from the stimuli used in the aesthetic judgment studies, they all possess a common feature of the directionality in their configurations (Figs. 1–3). That is, both the picture stimuli and vernier stimuli indicate either left-to-right or right-to-left directional cues. It can, therefore, be proposed that the preference for left-to-right directionality is not limited to the pictorial stimuli only; rather, it may occur in other visuospatial task depending on spatial organization or layout of the stimuli. Thus, as in the studies of aesthetic judgment of pictures, observers in vernier offset detection are perhaps predisposed to perceive a rightward offset vernier as aesthetically more pleasing than a leftward offset vernier.

Now, considering the findings of Karim and Kojima's (2010a,b) studies in the context of the studies reviewed in the prior section, Freimuth and Wapner's (1979) model can explain those findings

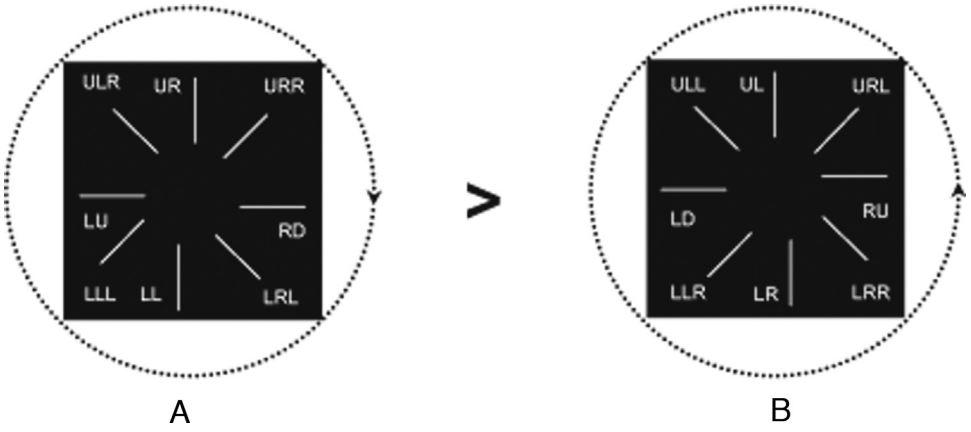

Fig. 3. Schematic of the directionality bias in vernier offset detection at different orientations. (A) 0°, 90°, +45° and −45° oriented configurations in which average performance was better; LU-RD = configuration at 0° orientation with Left feature Up vs. Right feature Down, UR-LL = configuration at 90° orientation with Upper feature to Right vs. Lower feature to Left, ULR-LRL = configuration at +45° orientation with Upper Left feature to Right vs. Lower Right feature to Left, URR-LLL = configuration at −45° orientation with Upper Right feature to Right vs. Lower Left feature to Left. (B) 0°, 90°, + 45° and −45° oriented configurations in which average performance was worse; LD-RU = configuration at 0° orientation with Left feature Down vs. Right feature Up, UL-LR = configuration at 90° orientation with Upper feature to Left vs. Lower feature to Right, ULL-LRR = configuration at +45° orientation with Upper Left feature to Left vs. Lower Right feature to Right, URL-LLR = configuration at −45° with Upper Right feature to Left vs. Lower Left feature to Right. The dashed circles with an arrow mark in the left and right portions of the figure indicate the clockwise (A) and anticlockwise (B) directionality of the offset stimuli (Source: Karim and Kojima, 2010b).

better than does the model of Levy (1976). As Levy (1976) posited, an attentional bias to the left makes a symmetrical picture look unbalanced and a picture asymmetric to the right look balanced. Though Levy did not explain what would happen if a picture is asymmetric in the same direction of the attentional bias, it is implied in her model that in such a situation the picture should look more unbalanced than is real. If this argument applies to the studies of Karim and Kojima, an attentional bias to the left and an offset to the left should make a vernier stimulus look more asymmetric and increase the likelihood of its correct detection. But, apart from that Karim and Kojima's results suggest that an attentional bias to the left and an offset to the right facilitate observer's detectability that the stimulus is offset or asymmetric. This indicates that Levy's concept of perceptual balance/imbalance might be incorrect. Thus, observers may prefer a stimulus asymmetric in the direction opposite to the attentional bias over the stimulus which is asymmetric in the same direction of the attentional bias, but it does not necessarily create any perceptual balance/imbalance. Why should attentional bias make a balanced picture look imbalanced and an imbalanced picture balanced? It would be surprising. Due to attentional bias, a balanced picture should of course be easily and more accurately detected as being balanced. Unfortunately Levy viewed the role of attention negatively which cannot be generalized to other situations of perception or perceptual learning. For example, Karim and Kojima's (2010a) study showed that subject's detectability of the rightward offset increased with training. Though Karim and Kojima, did not directly examined the impact of attention, other researchers have claimed that attentional effects on perception are subject to training (Ito et al., 1998); more training means more attentional resources and more neural changes which in turn should lead to more learning! Perceptual learning has been viewed as 'attention driven' (Ahissar and Hochstein, 2004) or dependent on attention for 'consolidation' (Gilbert et al., 2001). It interacts with attention under top-down control (Crist et al., 2001; Dosher et al., 2010; Gilbert et al., 2001) and perhaps becomes stabilized through training. According to Reverse Hierarchy Theory, the role of attention is to determine the cortical level where learning modification will take place (Ahissar and Hochstein, 2004). Attention modulates 'cortical self-organization and stability' (Grossberg, 2005), and is necessary to induce learning (Ahissar and Hochstein, 2000, 2004; Dosher et al., 2010; Roelfsema et al., 2010). Training improves perception, even in adults, only if they are willing to invest some effort in the task (Roelfsema et al., 2010). Learning of even very simple skills (e.g., vernier discrimination, orientation discrimination) requires task specific attention, and failure to attend the appropriate features of the stimuli results in no performance improvement (Ahissar and Hochstein, 1993; Harris and Fahle 1998; Shiu and Pashler, 1992; Tsushima and Watanabe, 2009). Thus attention gates perceptual learning (Ahissar and Hochstein, 1993; Baker et al., 2004; Jiang and Chun, 2001; Roelfsema et al., 2010; Turk-Browne et al., 2005). Though there are some forms of perceptual learning that may occur without attention (e.g., learning subliminal tasks or stimuli; for a review see Roelfsema et al., 2010; Seitz et al., 2005; Seitz and Watanabe, 2003; Watanabe et al., 2001), there is no reason to assume that attention has negative impact on perception or perceptual learning. Thus we argue that unlike Levy's theory the role of attentional bias should be positive in visuospatial perception and perceptual learning. Contrary to Levy's view, and the findings cited here and the explanations of the findings of Karim and Kojima about rightward directionality bias fits well with the view of Freimuth and Wapner (1979; see above). However, Freimuth and Wapner's model can also be problematic in applying to the stimuli at other geometric orientations. But, if a horizontally oriented stimulus is rotated clockwise or anticlockwise, then the left-to-right directionality will be equivalent to clockwise orientation, and the right-to-left directionality will be equivalent to anticlockwise orientation. So, if the idea of 'rightward (left-to-right)' direction is replaced by the term 'clockwise' direction and 'leftward (right-to-left)' direction by the term 'anticlockwise' direction then the problem is solved. In line with the findings in the past study (see above), it can be assumed that for a visuospatial stimulus suggesting directional cues visual attention and hence visual perception becomes 'clockwise' biased in the dextrals and 'anticlockwise' biased in the sinistrals. For a firm conclusion on the topic further empirical studies are necessary to conduct, using a variety of visuospatial stimuli across the orientations, though we will next review relevant work that supports this inference.

4. Directionality bias in space mapping or spatial coding

The left-right bias also occurs in both physical space mapping and mental space mapping. This has been well documented in a number of studies on pseudoneglect and related topics. Pseudoneglect refers to the fact that neurologically healthy individuals

typically favor the left side of space and therefore bisect a horizontal (tactile or visual) line to the left of the veridical center (Bowers and Heilman, 1980; for a metaanalytic review, see Jewell and McCourt, 2000), and this tendency is probably more pronounced among the males (Jewell and McCourt, 2000) and the right-handers (Jewell and McCourt, 2000; Scarisbrick et al., 1987). However, patients with hemispatial (unilateral neglect of the left side) and the elderly (Jewell and McCourt, 2000; Schmitz and Peigneux, 2011) tend to bisect physical lines to the right of center. This phenomenon is known as neglect. Recent studies have shown that pseudoneglect and neglect are not limited to physical stimuli but also extend to mental representations, such as in the bisection of mental number lines and mental alphabet lines. When perceiving numbers humans tend to spatially organize their magnitudes in ascending order on a left-to-right oriented number line, commonly referred to as the mental number line (Dehaene, 1997; Pasqualotto et al., 2014; Restle, 1970; Seron et al., 1992). Similarly, a left-to-right mental organization (i.e., in an ascending sequence of A–Z) is thought to occur for alphabets, called the mental alphabet line (Gevers et al., 2003; Nicholls and Loftus, 2007). Research has shown that similar to a physical line, individuals with an intact brain bisect the mental number line (Loftus et al., 2009) and the alphabet line (Nicholls and Loftus, 2007) reliably to the left and neglect patients bisect to the right (Nicholls and Loftus, 2007; Vuilleumier et al., 2004). Longo and Lourenco (2007) examined pseudonegect for both physical line bisection and mental line bisection in neurologically normal participants, and reported a highly correlated leftward bias for these tasks.

The concept of pseudoneglect may apparently seem to be contradictory to the concepts of the left-right biases discussed above, but it is actually not. We suggest that during space mapping or spatial coding we focus our attention initially on the left space where from it shifts to the right space (for details, see Sections 6 and 8). Research has shown that this left-right asymmetry can be related to lateral head turns, which are known to reallocate spatial attention in the outside world (Loetscher et al., 2008). That is, while facing left or turning anticlockwise humans tend to produce smaller numbers, whereas while facing right or turning clockwise they produce larger numbers (Loetscher et al., 2008; Fig. 4). A more recent study has also demonstrated similar findings for a group of normally sighted participants (Pasqualotto et al., 2014), indicating a close link between the asymmetry in spatial coding and head turning direction (for head turning direction, see the following section).

The origin of this left-right bias which is termed as pseudoneglect is primarily neurobiological. In support of this, functional neuroimaging evidence suggests that there is a topographical arrangement of numerical magnitudes in human parietal cortex (Harvey et al., 2013). Other studies suggest that like pseudoneglect for physical lines (Bjoertomt et al., 2002; Fierro et al., 2000; Foxe et al., 2003; Waberski et al., 2008), the neural basis of pseudoneglect for mental number line bisection appears to lie in the right posterior parietal cortex (Göbel et al., 2006). The direction of space mapping from left to right rather than vice versa might have been imposed by hemispheric asymmetry in the deployment of spatial attention (Rugani et al., 2010). In humans, treatment with dopamine (DA) agonists reduces the extent of unilateral neglect (Fleet et al., 1987), indicating that this asymmetric spatial attention might be caused by DA imbalance between the two hemispheres. Pseudoneglect or left-right bias in mental number lines is perhaps biologically rooted through evolution (Rugani et al., 2015a). Recent evidence of the presence of mental number lines in human newborns (de Hevia et al., 2014) and non-linguistic species (Drucker and Brannon, 2014; Rugani et al., 2007, 2010, 2015a,b) supports this notion. For example, de Hevia et al., (2014) demonstrated that seven-month-old infants prefer increasing (e.g., 1–3) to decreasing (e.g., 3–1) number magnitudes displayed from left to right,

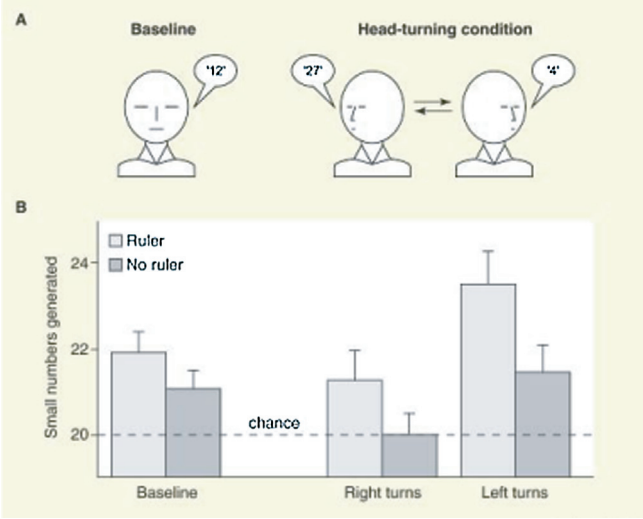

Fig. 4. Random number generation during head turning. (A) Each participant performed two runs, a baseline and a head-turning condition, in counterbalanced order. In the baseline condition, participants generated random numbers while keeping the head straight. In the head-turning condition (leftward or rightward), participants generated a random number at each turning point of the sinusoidal movement. Half of the participants received the instruction that imagination of a ruler with 30 units might facilitate their performance ('Ruler' group), whereas no such information was given to the remaining participants ('No ruler' group). (B) There was an increase in small numbers for left turns compared to baseline, but a decrease for right turns. Subjects in both groups generated significantly more small numbers after left turns than after right turns (From Loetscher et al., 2008, with permission).

indicating that it does exist before linguistic and mathematical education. Rugani et al. (2015a) demonstrated that 3-day-old domestic chicks, once familiarized with a target number (5), spontaneously associated a smaller number (2) with the left space and a larger number (8) with the right space, and interestingly, this last number was associated with the left space when the target number was 20. However, this does not necessarily undermine the role culture plays to foster numerical space mapping in a particular orientation. Studying congenitally blind, late onset blind and blind-folded sighted participants Pasqualotto et al. (2014) demonstrated that sensory deprivation can alter the mental number line, suggesting a role of visual experience in the development of numerical spatial coding in line with the cultural differences in number representation. This has been corroborated by the findings of other studies that the left-right bias in numerical space mapping can be reduced or even reversed in a culture that reads from right to left (e.g., Arabian, Palestinian). This suggests that the mental number line or the direction of space mapping can be altered or reshaped through culturally specific experiences (Jewell and McCourt, 2000; Shaki and Fischer, 2008; Shaki et al., 2009; Zebian, 2005).

5. Directionality bias in turning or rotational behavior

Another expression of functional asymmetry is the turning or rotational preference observed in both humans and non-human animals. In most of the past studies on turning or rotational behavior researchers used the terms leftward and rightward to refer to directional preferences. In this review we employed two new terms – clockwise and anticlockwise – to refer to directional preferences in a wide range of visuospatial behaviors. Like oriented or tilted visuospatial stimuli in which left-to-right directional cues or right facing stimuli refer to clockwise orientation and right-to-left directional cues or left facing stimuli refer to anticlockwise orientation (see Figs. 1–3), turning to the right (rightward) refers to clockwise and turning to the left (leftward) refers to anticlockwise orientation in most of the turning situations, such as turning head, walking a

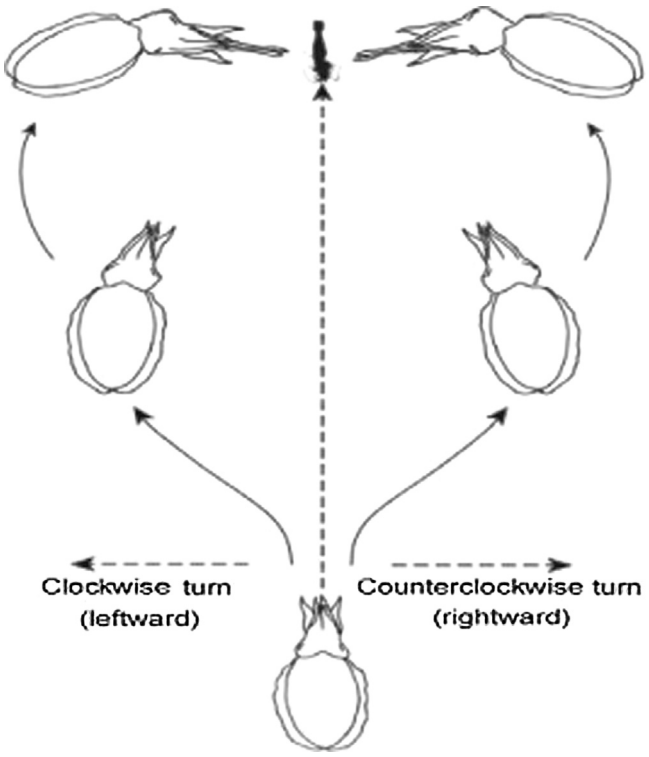

Fig. 5. Laterality of predatory behavior in cuttlefishes (*Sepia lycidas,* from Lucky et al., 2012; with permission).

straight line, moving in a plus-maze or T-maze. However, turning to the right or left cannot always be considered as a directionality bias. For example, if the target object is placed somewhere to the right or to the left of a person turning to the right or to the left, then her/his behavior will not exhibit any directionality bias because in such a situation everybody will probably turn to the direction following a principle of shorter distance. So, the concept of clockwise or anticlockwise direction in turning applies to the situation where the target/object is either in front or somewhere on the back side of the person, and there are only two trajectories, leftward and rightward (but no straightforward trajectory) to reach the target, with an equal distance on using either direction. Thus, in a situation where the target is in front of the person the direction of a trajectory and hence the directionality bias of the person (clockwise or anticlockwise) should be determined by considering the trajectory as a continuous whole, not in a discrete manner or just considering the initial turn only. For example, in case of turning or rotating in a circle or squared setting (e.g., entering a gallery or supermarket) an initial turn to the left will eventually create a clockwise rather than anticlockwise trajectory in the long run (hence the person will be considered as having a clockwise bias), and similarly an initial turn to the right will create an anticlockwise rather than clockwise trajectory (hence the person will be considered as having an anticlockwise bias; see Figs. 5 and 6). Now, if the person needs to get a target placed somewhere behind and its distance is equal on using either direction, the person's initial turn will be in a direction similar to the direction of the whole trajectory. However, below is discussed the experimental evidences for directional preferences in turning or rotational behavior in non-human animal and human organisms in a variety of situations.

Research in rats using the plus-maze or T-maze demonstrated asymmetries in turning direction in favor of the right/clockwise (Andrade et al., 2001; Schwarting and Borta, 2005). The findings in rodents have been supported by the findings of studies in fishes. For example, Bisazza and Vallortigara (1997) examined rotational preferences of mosquitofish (*Gambusia holbrooki*) in circular tanks with a group of females or a group of predators located at the center or during spontaneous swimming in absence of a specific target. It was demonstrated that mosquitofish swam preferentially clockwise in presence of the predators; however, no significant preferences appeared with the females or during spontaneous swimming in absence of a specific target. More recent research demonstrated that such a lateralization might also be apparent in predatory behavior. For example, it has been shown that lateralized fish perform better than nonlateralized fish when they are tested for their ability to capture shrimp in the presence of a predator; however, such a difference was not observed in the absence of a predator (Dadda and Bisazza, 2006). Consistently and very interestingly, Lucky and colleagues were the first to show directly the clockwise vs anticlockwise turning bias in young cuttlefishes (*Sepia lycidas*; Lucky et al., 2012). In a laboratory experiment, they investigated laterality in attacks on shrimps by cuttlefishes, and correlated this with morphological asymmetry as measured by the curvature of cuttlebone. Based on the curvature of cuttlebone they identified two categories of cuttlefishes: 'righties' and 'lefties'. 'Righties' are those cuttlefishes whose bones are convex to the right, and 'lefties' are those cuttlefishes whose bones are convex to the left. As expected, in line with this morphological asymmetry, 'lefties' tended to turn clockwise rather than anticlockwise, whereas 'righties' showed an opposite tendency in attacking the prey (Fig. 5). Similarly, in another study about 50% of the teleost fishes (*Jenynsia lineata*) were found to turn either right or left while escaping from predators (Bisazza et al., 1997). A couple of other studies showed that when adult cuttlefishes (*Sepia officinalis*) were allowed to freely move in a T-maze, some fishes tended to turn rightward whereas others turned leftward (Alves et al., 2007; Karson et al., 2003). Bisazza et al., (2001) studied turning preferences in fish using a variety of detour tests and demonstrated that the two different directions of lateralization exhibited by the right turning and left turning fishes were strongly and negatively correlated, and that there is a strong consistency among different tasks of left–right asymmetries. That is, the fish that turned to the right and those that turned to the left had a similar but left–right reversed pattern of subdivision of cognitive or behavioral functions which, according to the authors, is suggestive of a similarly left–right reversed (mirror image) brain organization. All these findings have been further corroborated in more recent studies. For example, Lippolis et al., (2009) found a rightward turning bias during feeding in the lungfish, the closest existing ancestor of the first land-dwelling vertebrates. Similarly, in a very recent review, MacNeilage (2014) demonstrated a wide range of evidences for the strong rightward action asymmetries (asymmetry in feeding) in marine mammals and in other vertebrates as well.

Like non-human animals, humans do also demonstrate directionality bias in turning or rotational behavior. This bias starts at some stage(s) during prenatal development and continues throughout the lifespan. In support of this, research has shown that human fetuses prefer to turn their heads to the right, rather than to the left, during the final weeks of gestation (Konishi et al., 1986; Ververs et al., 1994). This preference is also exhibited by newborns of both the vaginal and caesarean deliveries (Hopkins et al., 1987; Liederman and Kinsbourne, 1980a; Rönnqvist and Hopkins, 1998; Rönnqvist et al., 1998), and maintained for the first few months of birth (Konishi et al., 1986; Ververs et al., 1994). This earliest behavioral asymmetry is thought to predict later handedness (Gesell and Ames, 1947; Konishi et al., 1986; Michel, 1981; Previc, 1991), and also affect the subsequent development of perceptual, cognitive and motor preferences (Coryell and Michel, 1978; Konishi et al., 1987; Liederman and Kinsbourne, 1980a). These impacts can be predicted and well understood from observations of adult turning behavior in both artificial and natural environments. For example,

Bracha et al. (1987a) examined rotational movements in humans and demonstrated that normal humans of both sexes rotate preferentially to the left or to the right during a routine day. Males who were consistently right-sided in terms of handedness, footedness and eye dominance rotated more to the right than to the left, whereas females who were left-sided in terms of these types of laterality rotated more to the left than to the right. They further demonstrated that these rotational preferences had stability as measured on two occasions with a time interval of six weeks. More or less consistently, Previc and Saucedo (1992) demonstrated that more than half of the participants rotated rightward, and the direction and magnitude of turning correlated significantly with footedness and eyedness, but not with handedness.

A number of early studies reported that the paths taken by persons when walking a straight line blindfolded tend to veer to the right (Blumenthal, 1928; Brigden, 1935; Lund, 1930; Szymanski, 1913). A couple of other studies reported that veering direction is related to handedness or footedness (Day and Goins, 1997; Scharine and McBeath, 2002). However, more recent studies failed to show such a relationship and demonstrated a lack of stable or systematic directionality bias in veering behavior of humans. For example, Mohr and Lievesley (2007) examined veering behavior in healthy humans and found that veering side was not significantly related to handedness or footedness. None of the handedness (left, right, mixed) groups showed any side preference, and the stability of side preferences between two testing sessions (with a gap of four weeks) was low and unsatisfactory. Souman et al., (2009) examined walking trajectories in both blindfolded and sighted humans. They tested blindfolded participants in an outdoor experimental field, and sighted participants in two unfamiliar natural environments (a large forest area and the Sahara desert) when the sun was visible or invisible. They reported that for most blindfolded participants the walking trajectories were highly random, indicating little or no overall bias in walking direction. On the other hand, the sighted participants repeatedly walked in circles when the sun was invisible and sometimes veered from a straight line without forming any circle when the sun was visible. They concluded that veering from a straight line is the result of accumulating noise in the sensorimotor system which, without a reliable directional reference (e.g., landmarks or the solar azimuth), may cause people to walk in circles. Souman et al.'s work has been pioneering, yet it did not clarify whether participants preferred a clockwise or anticlockwise direction to walk in circles or to veer from the straight line. Also, it failed to control the presence of visual and other sources of sensory cues, such as moon, wind, heat or noises that might give an indication of walking direction or perturb walking due to ground irregularities (Bestaven et al., 2012). A more recent study in which all these potential variables were controlled found that 50% of the veering trajectories ended on the left, 39% on the right, and 11% were just straight (Bestaven et al., 2012). However, there was no significant difference in preference for right and left orientation when considering the overall trials, but substantial within-subject variability and between-subject variability from trial to trial were observed (Bestaven et al., 2012). The findings of the previous three studies have been corroborated by the findings of a very recent study that examined veering behavior in right-handed humans but under different experimental conditions (Consolo et al., 2014), In this study, participants were allowed to see the target for a brief period of time, then blindfolded, and asked to walk without any visual or auditory cues in an open field directly toward the target. This study demonstrated that irrespective the target distance, the most frequently used pattern was the circular trajectory. Analysis of the trajectories that deviated from the intended route revealed that 69% of the participants exhibited lateral orientation preference to the left rather than to the right when considering overall number of trials. However, most of the participants (93%) changed their side of deviation between trials, again indicating the unreliable nature of veering direction. In fact, this is a very special case of turning or rotational behavior in humans which occurs in the absence of external cues, and it should not be generalized to other cases of turning or rotational behaviors. We suggest that maintaining a straight-ahead direction or a specific preferred direction consistently across trials is perhaps impossible while walking or traveling in an environment without any visual, auditory or any other relevant cues. Perception does not occur in the absence of reliable sensory signals and without perceiving the world people cannot make a goal-directed (motor) behavior. In such a situation, people probably find themselves rendered helpless, which cause them either to stay (if not asked to walk/move) or to walk/move (if asked to do) in circles around their current standing positions (possibly within a short range of distance) rather than getting lost by walking toward an uncertain distant goal or target. However, researchers have suggested that this nature of veering can be caused by vestibular function (Consolo et al., 2014) rather than DA imbalance in the brain (Mohr and Lievesley, 2007).

Research in real life situations has shown that when kissing adult humans tend to turn their head rightwards that is, clockwise (Güntürkün, 2003). Based on his observations of 124 kissing couples (ages ranged from 13 to 70 years) in public places (international airports, large railway stations, beaches and parks) in the United States, Germany and Turkey, Güntürkün (2003) reported that of the 124 kissing couples 80 (64.5%) turned their heads to the right and 44 (35.5%) turned to the left. Thus the ratio of turning the head to the right and to the left was roughly 2:1. His result indicates that adults have a head turning bias towards the right side, just like embryos and newborns (Konishi et al., 1986; Ververs et al., 1994); however, this bias cannot be associated with handedness (Güntürkün, 2003). Subsequent studies in kissing couples or doll kissers have replicated the basic findings of Güntürkün (2003), with controversial evidence on the association of head turning bias with handedness or other types of lateral preferences. For example, unlike Güntürkün (2003) one study showed that there was an association of the direction of head-turning with handedness and footedness in doll kissers (Ocklenburg and Güntürkün, 2009) whereas in line with Güntürkün (2003) other studies in kissing couples (Barrett et al., 2006) or doll kissers (Barrett et al., 2006; van der Kamp and Canal-Bruland, 2011) demonstrated no clear relationship of this kind. However, apart from lateral preferences, a recent study which examined head turning bias in both kissing couples and doll kissers revealed that a rightward head turning bias in kissing was apparent in left-to-right readers (e.g., English) and a leftward head turning bias in right-to-left readers (e.g., Hebrew, Arabic; Shaki, 2013). This study concluded that the directional bias in head turning can be shaped by cultural spatial habits, rather than reflecting pre-wired hemispherical lateral asymmetry.

Karev (2000) conducted a study asking participants to select movie theatre seats from a seating chart. He reported that right-handed participants were more likely to choose a seat on the right side of the theatre than on the left side. This preference was reduced but not reversed in both left- and mixed-handed participants. A second study found the same results using a similar procedure (Weyers et al., 2006). The findings of both these studies have been replicated in a very recent study which investigated the real-world seating patterns of theatre patrons during actual film screenings and reported a significant bias to choose seats on the right side of the theatre (Harms et al., 2014).

The importance of 'clockwise' orientation has been well understood in Groeppel-Klein and Bartmann's (2008, 2009) recent studies on consumer behavior. One of their studies was conducted in two shops belonging to a discount grocery chain (n = 196, all right-handers). Both shops were identical in terms of assortment, prices and shoppers' familiarity with them. However, in one shop

customers were guided clockwise around the store and in the other they were guided anticlockwise. Before entering the shop, subjects had to locate eight specific products on central and peripheral aisles on a store map. Data were processed using a particular Geographical Information System (GIS; Burrough et al., 1988). The results showed that subjects in the store with clockwise layout had a more detailed mental map and evaluated the store better in terms of perceived ease of orientation and value for money. In addition, there was a significant correlation of the detailed mental map with both the ease of orientation and perceived value for money. In another study (n = 76, all right-handers), Groeppel-Klein and Bartmann (2008, 2009) looked at shoppers' travel and search patterns (Larson et al., 2005; Titus and Everett 1995) controlling shopping frequency and store patronage. Subjects were asked to shop eight specific products rather than just estimating their location, and two disguised observers kept track of the subjects' walking behavior. As in the first study, researchers used GIS to process data and to categorize subjects as 'short-distance shoppers' (who covered a linear distance of 5.81 m between the estimated and actual product location) and 'long-distance shoppers' (who covered a linear distance of 7.63 m between the estimated and actual product location). The results showed that significantly more shoppers took shorter distances to find out the products in the store with clockwise layout than in the store with anticlockwise layout. The 'short-distance shoppers' were also more efficient than the 'long-distance shoppers' in terms of accuracy of the mental map, time spent and the perceived ease of the task. They were also more willing to spend money than their counterparts. Furthermore, irrespective of shopper type, subjects in the clockwise layout needed less time and walked shorter distances than subjects in the counter-clockwise layout. Consistent with the psychophysical findings as above, all these real life studies clearly characterize visuospatial functioning as biased to the 'clockwise' direction.

However, in contrast to clockwise bias in turning behavior, some studies demonstrated that turning preference might occur in the opposite direction in both non-human animals and humans. For example, animal research has shown that anticlockwise/leftward turning predominates in swimming dolphins, Tursiops truncatus (Sobel et al., 1994), domestic chicks (Casey and Karpinski, 1999; Casey and Sleigh, 2001; Rogers, 1991), bobwhite quail (Casey and Sleigh, 2001), and ants (Hunt et al., 2014). Mohr et al. (2004) assessed in 36 healthy human participants long-term spontaneous turning (with a lightweight, rechargeable hip-mounted device consisting of a position sensor and an electronic processing circuit), veering (tendency to deviate from linearity when traveling or walking without any visual cues) and stepping (deviations while stepping blindfolded on a given spot) behavior. They observed a leftward preference for long-term spontaneous turning, but no directional preference for stepping or veering behavior as consistent with the other studies discussed above. More recently, Toussaint and Fagard (2008) tested spontaneous turning behavior in 13 human adults. Participants were required to run around a circle in an empty, symmetrical space, as a function of starting position (from the center, the left, or the right), and gaze direction (to one of five targets going from left to right). A clear significant overall tendency to turn anticlockwise across all conditions was observed. In this study, starting position, gaze and head direction were found to modulate the bias, without masking the anticlockwise tendency. Studies have further provided evidence for leftward turning preference in right-handers, with non-right-handers showing a bias towards the opposite direction (Mohr and Bracha, 2004; Mohr et al., 2003; Yazgan et al., 1996) or no bias at all (Yazgan et al., 1996). Thus far the evidence of directionality bias in turning behavior is inconsistent across studies. However, one thing is clear that in addition to a clockwise turning population there is always a second population showing anticlockwise turning or rotational preference; and that findings are possibly stronger and more numerous for a clockwise than for an anticlockwise bias.

6. A model for the directionality bias in visuospatial functioning: how perceptual bias is translated into a turning or rotational bias

Thus far we have shown evidence of the clockwise or anticlockwise bias in a variety of perceptual and motor tasks. These directionality biases perhaps reflect a directional element in the mental representations of both perceptual and motor processes. Though the tasks described here are of different kinds they have a number of common features. Specifically, most of them are visuospatial and some are spatial (e.g., walking with a blindfold) tasks and have a common feature of directionality in their spatial layout or organization (Figs. 1–3). All these tasks perhaps require an identical mental representation, irrespective of their processing levels (early or late), which is mostly biased to the clockwise direction. Thus, regardless of whether one is engaged in a perceptual task (e.g., aesthetic appreciation, line alignment, line bisection) or a motor task (e.g., turning or rotating task), a common directionality in the preferred mode of representation may lead to consistent biases in behavior. A few lines of evidence provide partial support for this view. For example, it has been shown that French readers (left to right) showed a greater tendency to bisect a line to the left of its center (Chokron and De Agostini, 1995), and preferred images that displayed a left-to-right directionality (Chokron and De Agostini, 2000). In a similar vein, Hebrew readers (right to left) showed a greater tendency to bisect a line to the right of its center (Chokron and De Agostini, 1995), and preferred images with a right-to-left directionality (Chokron and De Agostini, 2000). Though the participants of these two studies were not the same they came from the same cultures (French and Israeli), indicating that there might be a link between asymmetry in line bisection and asymmetry in picture viewing. In addition, as we have seen earlier in this review, the left-right bias in random number generation can be associated with head turning direction (with small numbers envisaged to the left turn, and large numbers to the right turn; Loetscher et al., 2008; Pasqualotto et al., 2014). This indicates that the asymmetry in space mapping (spatial mental bias) has a close link to the direction of head turning (though it is not tested yet in a preferred turning mode).

Seeing and perceiving clockwise is perhaps the parsimonious and convenient way of understanding the surrounding for the majority of us. In an environment where we need to turn, we do not turn directly: first we see, scan and perceive the environment clockwise (Stage 1); form a mental map of its spatial organization clockwise (Stage 2); and then turn to the same direction (Stage 3). We call this process as 'Perception (of spatial-mapping)-Action-Laterality (turning)' or simply '*Perception-Action-Laterality*' hypothesis as shown in Fig. 6. In this figure, the person, P, is standing in a place directly facing to the target room, T; from his standing point the distance of the target is the same if used either of the two alternative routes, LADL and RBCR. Now, if the person prefers, say, a clockwise trajectory he will first turn to the left at his standing point, walk to the left for a while until the first corner, A, then turn to the right, walk again straight until reaching the second corner, D, where he will turn to the right and walk straight to the target room, T. Though the person will make an initial turn to the left the next two turns will definitely be rightward until reaching the target. We argue that he has actually a clockwise or rightward directionality bias; he makes the initial turn leftward in order to produce a full rightward or clockwise trajectory. Thus considering his trajectory as a continuous whole (see Section 5) we can classify the person as a clockwise turner. This trajectory enables him to see

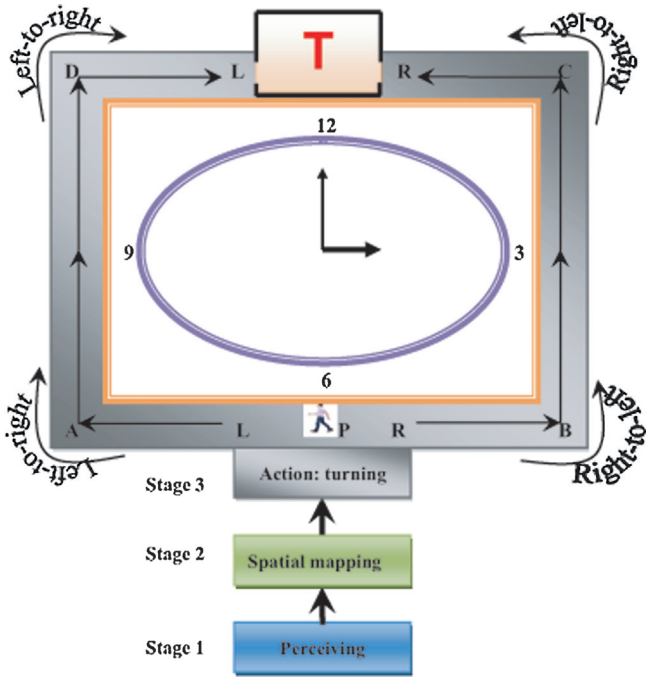

Fig. 6. A three-stage (*Perception (of spatial-mapping)-Action-Laterality (turning)*) model of directionality bias in visuospatial functioning. P = Person who perceives the world, develops spatial maps, and/or turns to a particular direction; T = Target room; L = Left side of P or T; R = Right side of P or T; LADL shows a clockwise (left-to-right) trajectory from P to T; RBCR shows an anticlockwise (right-to-left) trajectory from P to T.

and perceive the target better as it is always at his right side (and, of course, this idea is also consistent with those who prefer the opposite direction). Once entered into the target room the person will probably follow the same principle of turning or the principle of shorter distance towards another target, if needed, in the room. The former part of this argument is consistent with the demonstration that humans have a tendency to turn right upon entering a room (Scharine and McBeath, 2002).

However, due to an innate head turning bias to the right in humans (discussed in previous section) readers may assume, contrary to this model, that turning behavior is followed by perceptual and cognitive processes. But, this is probably not the case in whole body turning. We argue that the innate rightward directionality bias in head turning promotes visual orientation to the right side (Coryell and Michel, 1978; Konishi et al., 1987), helping us first to perceive the right side better, form a spatial map, and decide to turn or not to turn (the whole body) depending on the situation. If the situation favors we spontaneously turn to the preferred direction; if the situation does not favor, such as in the presence of noxious/dangerous stimuli/objects (e.g., snake, chaotic publics) somewhere in the preferred direction, we do not turn or if we turn we do it to the opposite direction. In other words, in order to move around in our environment, we perceive and map the locations and orientations of the objects or stimuli relative to our self, have sense and act upon these objects or stimuli, and then move through space in a preferred direction, such as clockwise, to position ourselves in a safe location or in a non-preferred direction, such as anticlockwise, to avoid a dangerous location. However, in situations that do not require immediate turning behavior we just perceive the situations (or stimuli) and develop a mental map in a preferred direction, such as clockwise direction, which may or may not translate later into motor actions depending on environmental demands. For example, if we have oriented visual objects or stimuli in front of us as in Figs. 1–3 we just sense, perceive and map the objects or stimuli clockwise or anticlockwise depending on our spatial preferential mode. For the perception and space mapping of the static objects or stimuli which do not give us any motor stimulation or require any bodily movement perhaps our mental rotation still operates in a preferred direction or orientation of the objects/stimuli. According to this spatial mapping model, mental representations of perceptual objects contain an inherent directionality that can be related to such findings as perceptual anisotropies in processing rightward or clockwise-oriented objects/stimuli relative to leftward or anticlockwise-oriented objects/stimuli (e.g., Freimuth and Wapner, 1979; Karim and Kojima, 2010a,b,c; McLaughlin et al., 1983; Mead and McLaughlin, 1992). Also, rightward or clockwise turning behavior is just a translation of our rightward or clockwise bias in perceptual and cognitive representation. This kind of spatial mapping can probably be robust for both the head and whole body turning in other types of visuospatial functioning. Thus most people turn their head clockwise while kissing (Barrett et al., 2006; Güntürkün, 2003; Ocklenburg and Güntürkün, 2009; Shaki, 2013; van der Kamp and Canal-Bruland, 2011), and turn their body clockwise while shopping in a supermarket (Groeppel-Klein and Bartmann, 2008, 2009).

7. A dynamic model for the origins of directionality biases in visuospatial functioning

Why are the biases in visuospatial functioning clockwise in most humans or non-human animals and anticlockwise in others? Why are there still some people or organisms showing no bias at all? Shortly speaking, how is the bias developed? By revisiting and analyzing the literature on behavioral and functional laterality of the brain for both humans and non-human animals we will try to find out some comprehensive answers to these sorts of questions below.

Research has shown that the rightward bias in head turning is more frequent among the children of two right-handed parents (Liederman and Kinsbourne, 1980c). So, one source of clockwise bias in humans may stem from handedness. Because about 90% of individuals are right handed (Coren, 1992) directional bias in visuospatial perception and motor behavior may simply reflect the preponderance of right-handed people. Empirical evidence goes in support of this. For example, an inspection of the individual data of Karim and Kojima's (2010a,b) studies indicates that a greater proportion of the participants tended to show clockwise bias in vernier offset detection. Though they did not provide any handedness data of the participants, direct evidence of a link of the directional bias to handedness comes from studies on aesthetic appreciation and turning/rotational behavior. Specifically, as mentioned earlier in this review, right-handers prefer pictorial arrangements possessing left-to-right directionality (e.g., Beaumont, 1985; Freimuth and Wapner, 1979; Levy, 1976; Mead and McLaughlin, 1992) whereas left-handers typically exhibit preferences for patterns having right-to-left directionality (e.g., Banich et al., 1989; Christman and Dietsch, 1995; Levy, 1976; Mead and McLaughlin, 1992).

As discussed earlier about rotational behavior, Bracha et al., (1987a) observed in both males and females to preferentially rotate to the left or right during a routine day. In this study, leftward bias was more pronounced in left-hemisphere dominant females whereas rightward bias was more pronounced in right-hemisphere dominant males. Mead and Hampson (1996) asked right-handed participants to turn towards a beep that was played in half of the 160 trials directly from behind and in half of the trials from either the left or the right of them. They found a consistent rightward turning bias that was more pronounced in females. On the other hand, Previc and Saucedo (1992) used a stepping task and observed that slightly more than 50% of their participants, when deprived from

visual or auditory input, exhibited a rightward bias after stepping for 1 min on the spot. The degree of bias was significantly correlated (though the correlation size was low) with foot preference and eye preference, but not with handedness. Bradshaw and Bradshaw (1988) conducted a free-field observational study in which participants were required to rotate 720° clockwise or anticlockwise. The results demonstrated that dextrals, especially female dextrals, preferred to turn clockwise, while sinistrals showed an anticlockwise bias. When participants were blindfolded and walked in a straight line, all of them deviated to the right, the effect being slightly larger for females and dextrals. It is thus possible that handedness may bias people to see and turn toward their favored hand, though a few studies reported a turning bias in an opposite direction (Mohr and Bracha, 2004; Mohr et al., 2003; Yazgan et al., 1996).

The role of handedness, footedness, and sex in determining the direction of movement or rotation (clockwise or anticlockwise) in humans have been further corroborated by the findings of a very recent study conducted by Stochl and Croudace (2013) on a very large sample (1526) collected from 97 countries. They measured participants' preference for clockwise or anticlockwise rotation (drawing a circle, stirring a pot, jumping and spinning, rotation when looking behind, and practical turning) by using a five-item questionnaire. Through exploratory and confirmatory factor analyses of the data they identified two types of human movements or rotations: local versus global. As they demonstrated, handedness, footedness, and hemispheric lateralization (using the spinning girl silhouette) predicted the direction of both global and local rotations. Geospatial location or Coriolis predicted the direction of neither global nor local rotation, and sex predicted the direction of global but not local rotation. Both males and females rotated clockwise, but females showed significantly greater tendency to rotate clockwise than males during global rotation. However, we propose that the preference to see and turn to the right (i.e., clockwise) can also be attributed to the dominant right eye having a better view of the right side. Thus hand dominance and eye dominance together contribute to make our perception and turning better at clockwise orientation. In support of this idea, Adams (1965) found that baseball players whose dominant hand and dominant eye were on the same side appeared to adjust their batting stances in order to allow the dominant eye to better see the approaching ball. However, not all studies reported the impact of eye dominance on directional preference in turning behavior (e.g., Scharine and McBeath, 2002).

Other studies in humans have shown that the right hemisphere has dominance over the left hemisphere in the left (visual) field for spatial attention and spatial processing (Corbetta et al., 1993; Heilman and Van Den Abell, 1979; Mattingley et al., 1994). Related to this is the impact of neurochemical laterality (e.g., dopaminergic imbalance between the two hemispheres). It has been suggested that our visuospatial attention (e.g., Tomasi et al., 2009) and direction of turning or rotation (see Mead and Hampson, 1996; Mohr et al., 2004; Shi et al., 2014) depend on the integrity of the DA system. Thus in addition to the gross-level laterality indexed by handedness, footedness, and eye dominance, neurochemical laterality of the brain (Ocklenburg and Güntürkün, 2012; Toga and Thompson, 2003) as well as neurogenetic factors (for details, see the following section) can play a crucial role in the development of directionality bias in visuospatial functioning in humans.

The directionality biases in visuospatial functioning cannot be explained only by neurobiological or neurogenetic factors (for a review, see Jewell and McCourt, 2000). Many of our visuospatial asymmetries are determined or affected by environmental or cultural factors, such as scanning (reading/writing) habits and traffic rules. Nachshon (1985) conducted an experiment on Hebrew-, Arabic-, and English-language readers, asking them to reproduce various shapes. In this experiment, native English-language readers showed left-to-right directionality, and native Hebrew- and Arabic-language readers showed right-to-left tendencies in drawing the shapes. Reading direction can also affect the direction of head-turning in humans. In support of this, Shaki (2013) demonstrated a rightward head-turning bias during kissing in couples in countries with left-to-right reading habits (e.g., Western), and a leftward head-turning bias in countries with right-to-left reading habits (e.g., Middle-Eastern). The impact of traffic rules has been shown in a study (n = 112) by Scharine and McBeath (2002). This study used a T-maze where participant's task was to find a target hidden in either the left or right hand side of the T part of the maze. They showed that driving-side rules significantly influenced turning behavior in a simple 'T-maze' task. American participants favored turning to the right, English participants favored turning to the left, the number of right-turners was significantly higher than the number of left-turners, and the right-handers were more inclined to bear the right than were the left-handers. Their findings further indicate that handedness was the strongest predictor of turning direction, followed by the side of the road driven on (Table 2). However, the proportion of the people with clockwise bias did not correspond to the proportion of right-handedness in the population as cultural factors might have modified or altered the original 9:1 pattern based on the proportion of right- and left-handers in the population at large (Coren, 1992). That is, the proportion of participants in each category (Table 3) is not reflected in the proportion of participants turning right by laterality condition (Table 2).

However, there is a lively debate prevailing on the roles of the two forces of influence (neurobiological and cultural) for the development of directionality biases in visuospatial functioning. As discussed earlier in this review, some studies showed that the degree of preference for a top-left lighting condition in a 3D shape perception can be determined by handedness (Sun and Perona, 1998) whereas other studies claimed that this can be determined by cultural factors (e.g., reading direction), rather than handedness (Andrews et al., 2013). Ocklenburg and Güntürkün (2009) demonstrated that the direction of head-turning in human adults can be associated with handedness or footedness (e.g., Ocklenburg and Güntürkün, 2009) whereas Shaki (2013) found that this can be shaped by cultural spatial habits, such as reading direction. Similarly, some studies found the effect of handedness on directionality bias in aesthetic perception (Banich et al., 1989; Beaumont, 1985; Christman and Dietsch, 1995; Freimuth and Wapner, 1979; Levy,

Table 2
Proportion of participants turning right by laterality condition.

Source of laterality	Proportion of participants turning rightward	
	Left	Right
Handedness*	33.3%	66.0%
Side of road driven on*	46.7%	67.1%
Side of page written language begins on	60.2%	55.6%
Dominant eye	61.8%	61.5%

Source: Scharine and McBeath, 2002.
* $p \leq 0.05$.

Table 3
Proportion of participants in different categories.

Source of laterality	Proportion of participants studied	
	Left	Right
Handedness	13.4%	86.6%
Side of road driven on	26.8%	73.2%
Side of page written language begins on	92.0%	8.0%
Dominant eye	39.5%	60.5%

Source: Scharine and McBeath, 2002.

1976; Mead and McLaughlin, 1992) whereas other studies reported a strong effect of reading habits, with left-to-right readers showing a preference for stimuli with a rightward directionality while right-to-left readers preferred stimuli with a leftward directionality (for details see earlier in this review; Chokron and De Agostini, 2000; Friedrich and Elias, 2016; Friedrich et al., 2014; González, 2012; Ishii et al., 2011; Maass et al., 2007; Nachson et al., 1999). Other studies have further suggested that handedness and reading or writing habits can influence the preferred directionality in an interactive fashion, not only in visual perception but also in drawing figures. For example, Shanon (1979) compared right- and left-handed American and Israeli (left-to-right vs right-to-left) readers using graphomotor and drawing tasks. He demonstrated that the directionality of right-handers with either reading habit seems determined by biological factors whereas left-handers are more influenced by environmental factors and exhibit compromises when these are in conflict with the biological factors. Singh et al., (2000) showed that children are able to draw lines from left-to-right using either hand more accurately than those drawn from right to left, and this was particularly true for right-handed left-to-right users. Though the bidirectional readers showed no directional bias they performed the tasks more accurately than did their unidirectional counterparts. Similarly, Vaid et al. (2002) examined the relative influence of handedness and reading or writing direction on the direction of stroke in drawing figures like a tree, a hand, a house, an arrow, a pencil, and a fish. They studied adult readers of opposing reading directionality (Hindi vs Urdu) and found that right-handers (both literates and illiterates) and left-to-right readers drew most figures in a left-to-right direction whereas left-handers (both literates and illiterates) and right-to-left readers more often drew the figures from right to left.

Thus there are two opposing views on the development of directionality biases in visuospatial functioning. According to one view, directionality biases are developed due to functional and neurochemical laterality (hemispheric imbalance) of the brain whereas a second view posits that the biases derive from culturally bound driving or scanning habits associated with the direction of driving or with the way in which language is written and read in a particular society. Taken together, we propose that for the development of a bias the two forces of influence (neurobiological and cultural) work in an interactive rather than mutually independent fashion. More precisely, in order to determine directionality biases in visuospatial functioning, the unlearned, neurobiological or neurogenetic factors indexed by lateralization (handedness, footedness, eye dominance, genetic or neurochemical asymmetry) that have been probably evolved through evolution (Duboc et al., 2015; Lalan, 2008; MacNeilage et al., 2009; Rogers and Vallortigara, 2015; Vallortigara et al., 2011) interact in a very complex and dynamic manner with the learned factors (reading/writing direction, traffic rules), under 'cultural' practice or 'social' selection pressure (Ghirlanda and Vallortigara, 2004). This interaction probably occurs in a biased competition framework where the extent and direction of biases and the proportion of biased people in the population are determined, by the relative strength and direction of the two forces of influence, via neural plasticity of the brain (analogous to the biased competition process used to determine attentional allocation in perception; cf. Desimone and Duncan, 1995; Proulx and Egeth, 2008). The neurobiological or neurogenetic factors, such as genes, lay the foundation for perceptual and functional asymmetry and experience received through cultural transmission determines the extent to which the asymmetry can be achieved (Rogers and Vallortigara, 2015). Research has shown that despite cultural similarities between the samples, native left-to-right readers demonstrated a strong preference for stimuli with left-to-right directionality whereas right-to-left readers failed to demonstrate such a bias (Friedrich and Elias, 2016). Treiman and Allaith (2013) failed to find a significant difference between native left-to-right and right-to-left readers' aesthetic preference for images of static and mobile objects. This pattern of results provides evidence that the strength and direction of aesthetic bias seeded biologically can be influenced (fostered or altered) by environmental or cultural factors, such as driving habits in a particular direction or scanning habits developed from reading/writing direction.

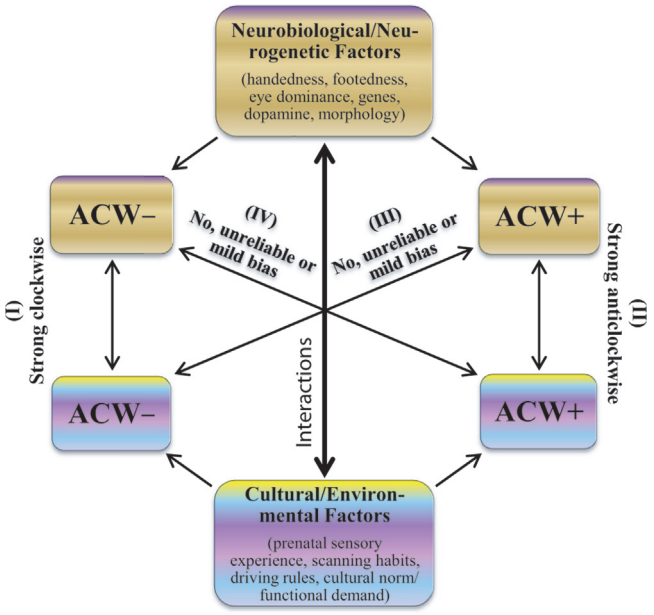

Fig. 7. A hypothetical model of the interactions between neurobiological or neurogenetic factors and environmental or cultural factors that determine the direction and extent of biases in visuospatial functioning. ACW refers to anticlockwise, '+' stands for favorable, and '–' stands for unfavorable. So, 'ACW+' indicates that the factors favor the development of an anticlockwise bias, and 'ACW–' indicates that the factors inhibit the development of an anticlockwise bias in favor of the clockwise. (I) Both neurobiological/neurogenetic factors and environmental/cultural factors inhibit the development of an anticlockwise (ACW– –) bias, in favor of a strong clockwise bias. (II) Both neurobiological/neurogenetic factors and environmental/cultural factors favor the development of an anticlockwise (ACW+ +) bias, promoting the person to be strongly anticlockwise. (III) Neurobiological/neurogenetic factors favor the development of an anticlockwise bias against the clockwise influences of the environmental/cultural factors (ACW+ –), leading the person to be unbiased, unrelaibly or mildly bias to some direction (for an explanation of the strength and direction, see the text in this section). (IV) Environmental/cultural factors favor the development of an anticlockwise bias against the clockwise influences of the neurobiological or neurogenetic factors (ACW– +), leading the person to be unbiased, unreliably or mildly bias to some direction (for an explanation of the strength and direction, see the text in this section).

We depicted the dynamic model of interactions between the neurobiological and cultural factors in Fig. 7, showing the possible outcomes of the interactions. Though the actual interactions between the factors are not as simple (Bracha et al., 1987a) as we have illustrated in this figure we believe that it helps understand how the two forces of influence interact to determine the direction and extent of bias a person may develop in visuospatial functioning. According to this model, the two classes of factors act either in concert or in conflict, the person being impacted in one of the four possible ways. One possibility is that both the neurobiological and cultural factors act in concert to inhibit or block the development of an anticlockwise (ACW– –) bias in favor of a strong clockwise bias. For example, if a person-P1 has DA dominance in the left hemisphere (which motivates people clockwise; for details, see the following section), exposing her/him to an environment or cultural milieu with left-to-right reading/writing habits, when the influences of all other factors are constant, will accelerate her/his biologically seeded preference for stimuli (e.g.,

aesthetic stimuli) oriented clockwise, and also turning or rotational behavior in a similar direction. Studies which demonstrated strong rightward/clockwise biases in a culture favoring right handedness and/or left-to-right scanning habits perhaps support this possibility (see Section 2; Chokron and De Agostini, 2000; Friedrich et al., 2014; Friedrich and Elias, 2016; Ishii et al., 2011; Nachson et al., 1999). A second possibility is that both the neurobiological and cultural factors act in concert for the development of a strong anticlockwise (ACW+ +) bias. For example, if a person-P2 has DA dominance in the right hemisphere (which motivates people anticlockwise; for details, see the following section), exposing her/him to an environment or cultural milieu with right-to-left reading/writing habits, when the influences of all other factors are constant, will accelerate her/his biologically seeded preference for stimuli (e.g., aesthetic stimuli) oriented anticlockwise, and also turning or rotational behavior in a similar direction. Studies which demonstrated strong leftward/anticlockwise biases in a culture favoring left handedness and/or right-to-left scanning habits perhaps support this possibility (see Section 2; Chokron and De Agostini, 2000; Friedrich et al., 2014; Friedrich and Elias, 2016; Ishii et al., 2011; Nachson et al., 1999). A third possibility is that the neurobiological factors favor the development of an anticlockwise bias against the clockwise influences of the cultural factors (ACW+ −), leading the person to be unbiased, unreliably biased, or mildly bias to some direction. If the person-P2 is exposed to a culture with left-to-right instead of right-to-left reading/writing habits this will be conflicting with her/his DA activity and will probably alter its function (depending on how strong is the cultural influence), and reorganize the neural networks (other factors being equal), reducing her/his biologically seeded leftward/anticlockwise preference. Finally, a fourth possibility is that the cultural factors favor the development of an anticlockwise bias against the clockwise influences of the neurobiological factors (ACW− +), leading the person to be unbiased, unreliably biased or mildly biased to some direction. Now, if the person-P1 is exposed to a culture with right-to-left instead of left-to-right reading/writing habits this will be conflicting with her/his DA activity and will probably alter its function (depending on how strong is the cultural influence), and reorganize the neural networks (other factors being equal), reducing her/his biologically seeded rightward/clockwise preference.

We have explained the first two possibilities backed by some previous studies above. However, the knowledge we currently have based on laterality research is too little to explain the last two possibilities. Theoretically, as suggested above, individuals in these two categories will be unbiased, unreliably biased or mildly biased to some direction, assuming that the two opposing forces of influences will neutralize or minimize each other's influence during the course of interactions. Studies that demonstrated no or unreliable biases or mild level of biases lend support for these possibilities. However, going beyond this assumption, we cannot preclude the possibility that an individual may also be strongly biased even in these two counteracting situations if the influences of either class of factors are strong enough to overwhelm the counter influences of the other class of factors. In such a situation, the direction of bias (if there is any) will be in a direction of the factors that win the biased competition during the course of interactions. Thus if the neurobiological influences are favorable for an anticlockwise bias and dominate over the unfavorable cultural influences the person may have an anticlockwise bias, but if the dominance is captured by the cultural factors the person may have a clockwise bias. Similarly, if the cultural influences are favorable for an anticlockwise bias and dominate over the unfavorable neurobiological influences the person may have an anticlockwise bias, but if this dominance is captured by the neurobiological factors the person may have a clockwise bias.

A recent study demonstrated that Bahraini students preferred right-facing pictures rather than those that faced in the direction of their writing system (Treiman and Allaith, 2013), indicating that perhaps the influence of neurogenetic factors overwhelmed the counter influence of cultural habits (reading direction), and the resulting impact was the person having a clockwise/rightward bias. However, in the unlikely event that the environmental or cultural transmission is unbiased/neutral then the direction and extent of bias in visuospatial functioning is solely determined by the direction and strength of the neurobiological influences (e.g., laterality, neurogenetic or neurochemical asymmetry) and vice versa. Thus as result of dynamic interactions between the two forces of influences (neurobiological and cultural) some people become strongly biased, some become mildly biased while others become unbiased or unreliably biased. However, as evidenced above and earlier in this review, most of the people are biased either clockwise or anticlockwise.

Now, how can this model explain the directionality bias in model organisms? As in humans, both neurobiological and cultural or environmental factors but not necessarily the same factors interact to determine the directionality bias in non-human animals. This argument is particularly true for the environmental factors because animals do not necessarily have the same culture or environment as do humans. In the previous section, we have seen that turning or rotational preferences in non-human animals vary widely from species to species. This suggests that their turning preferences are perhaps caused by different factors. For example, the factors of reading or scanning direction and traffic rules do not apply for non-human animals. Researchers hypothesized that lateralization of some forms of visual behavior (leftward or rightward directionality bias) can be generated in avian species, such as pigeons and domestic chickens, by exposing the developing embryos to biased prenatal sensory experiences (unilateral light stimulation to one eye just before hatching; Casey and Sleigh, 2001; Manns and Strökens, 2014; Rogers, 1990, 1991). Additionally, chicks hatched from eggs incubated in completely dark conditions do not develop any asymmetry in the visual pathways and visual behavior in categorization of food items and in responding to predators (Rogers, 2012). Light exposure during embryonic development also affects the development of lateralized behavior in zebrafish (Budaev and Andrew, 2009) and in cuttlefishes it is caused by morphological asymmetry of the cuttlebone (Lucky et al., 2012). However, we are not precluding the possible contributions of the general factors that may cause directionality bias in non-human animals as in humans. The factors that are most commonly considered to cause a bias in both humans and animal species are neurogenetics, handedness and other kinds of laterality rooted biologically through evolution (Lalan, 2008; Vallortigara et al., 2011), albeit their influences can be shaped by cultural, ecological and functional demands (for a review see Versace and Vallortigara, 2015) due to cortical plasticity. In support of this, research has shown that handedness (asymmetry of limb usage) and asymmetries in neural coding are not limited to humans only, rather they are present in a variety of vertebrate and invertebrate species (Duboc et al., 2015; Dreosti et al., 2014; Frasnelli, 2013; Frasnelli et al., 2012; Rigosi et al., 2015; for a review see Vallortigara et al., 2011; Versace and Vallortigara, 2015).

Though the final behavioral outcome of a person or non-human organism is determined by complex interactions between the two forces of influence (Fig. 7), we discuss in the following two sections the role of neurobiological or neurogenetic factors and the modulatory role of cultural factors, showing with empirical evidence how they tend to make their own contributions to the development of perceptual, cognitive and behavioral biases in both humans and non-human animals.

8. Neurobiological or neurogenetic bases of the visuospatial directionality bias

The neural basis of directionality bias in visuospatial functioning has been well documented in both non-human animal and human studies. The evidence for turning the head to the right in neonatal rats (Afonso et al., 1993), human fetuses (Konishi et al., 1986; Ververs et al., 1994), and human newborns (Hopkins et al., 1987; Liederman and Kinsbourne, 1980a; Rönnqvist and Hopkins, 1998; Rönnqvist et al., 1998) clearly indicates an underlying neural bases of the directionality bias in turning or rotational behavior. Research has shown that the rightward bias in head turning is more frequent among the children of two right-handed parents (Liederman and Kinsbourne, 1980c), indicating the heritable nature and genetic bases of the bias. The heritability of handedness in humans (Annett, 1973; McManus and Bryden, 1992; Medland et al., 2010) and forelimb preferences (Versace and Vallortigara, 2015) and morphological asymmetries (Bisazza et al., 2000; Namigai et al., 2014) in vertebrates, and their demonstrated relationships to the directionality bias in visuospatial functioning do also suggest a potential genetic endowment of the asymmetrical behavioral pattern. In support of this, research in cichlid fish has demonstrated that the direction of mouth-opening (either left-handed or right-handed) is determined on the basis of simple genetics (Hori, 1993), and that the behavioral asymmetries can be inherited in both strength and direction (Bisazza et al., 2000). One potential genetic endowment for the development of left-right asymmetry in different organs or tissues is perhaps Transforming Growth Factor Beta (TGFβ), also known as Nodal signaling module (Namigai et al., 2014). Recent studies have reported that Nodal pathway is involved in the development of left-right asymmetry in vertebrates (Boorman and Shimeld, 2002a,b; Duboc et al., 2015; Nakamura and Hamada, 2012; Soukup et al., 2015). Research in zebrafish has shown that the Nodal pathway has a role in the development of both visceral and neural asymmetry (Halpern et al., 2003; Roussigne et al., 2012), and when expression of this pathway is absent, structural asymmetries in zebrafish are maintained but they are random in direction (Concha et al., 2000). It has been suggested that the Nodal pathway can also be involved in the development of human handedness (Brandler and Paracchini, 2014), and that for the presence of this gene the direction and strength of biases may represent independent phenotypes (Ocklenburg et al., 2014). However, it remains to be investigated whether this gene is really involved in the genesis of such an asymmetry in humans and invertebrates as well.

The evidence for neurobiological or neurogenetic bases of the directionality bias in visuospatial functioning further comes from a number of lesion studies in non-human animals and dopaminergic gene studies in humans with intact brains. In a lesion study of Glick and Cox (1978), rats were first allowed to rotate under free-field conditions in circles at night. When they showed stable patterns of rotation unilateral lesions were made in either the substantia nigra, the nigrostriatal bundle or the caudate nucleus. All these lesions produced contralateral rotation in rats. The magnitude of contralateral rotation was correlated with lesion size, and was greater if the lesion was in the side of the brain opposite to the preoperative direction of rotation than if in the same side. Similar results were observed when unilateral lesions were done in medial forebrain bundle of rats (Lebsanft et al., 2003) or unilateral hemispherectomy was done in adult mice (Krahe et al., 2001). A very recent study examined grooming behavior (an innate set of stereotyped movements affecting all parts of body, Spruijt et al., 1992) in mice unilaterally lesioned in the medial forebrain bundle by 6-hydroxydopamine (Pelosi et al., 2015). This study showed that such a lesion of DA neurons induced grooming asymmetry, with reduced tendency to groom the contralateral side to the lesion, and that the symmetry of grooming can be recovered by increasing DA concentration with L-DOPA. Perhaps related to this is the evidence that lesions of the ascending dopaminergic pathways cause neglect-like behavior in rats (Iversen, 1984) while in humans treatment with DA agonists reduces the extent of unilateral neglect (Fleet et al., 1987).

The findings of lesion studies have been further corroborated by the findings of recent studies in humans with intact brains which revealed that functional genetic variants within dopaminergic genes contribute to orienting biases (the direction of attention in space). For example, a couple of studies in visual orientation or visual attention have shown that the Dopamine Transporter (DAT1) gene significantly influenced spatial bias in healthy children (Bellgrove et al., 2007; Newman et al., 2012). In Bellgrove et al.'s study (2007) healthy children who were homozygous for alleles that influence the expression of DA transporters in the brain displayed inattention for left-sided stimuli, but heterozygotes did not. Thus they showed evidence in healthy individuals of a genetically mediated bias in spatial attention that is related to DA signaling. A very recent study with normal human adults showed that allelic variation in a common polymorphism of the DAT1 gene was linked to a lateralized attention but not to response selection (Newman et al., 2014). That is, DNA variation in a putatively functional DA polymorphism was associated with enhanced attentional selection, particularly for stimuli presented within the left hemifield. Another very recent study demonstrated that homozygous carriers of the A2 allele displayed significantly greater leftward orienting bias than the carriers of the A1 allele, and the carriers of the 9-repeat allele (of the DAT130 VNTR) displayed significantly greater leftward orienting of attention than those who were homozygous for the 10-repeat allele (Zozulinsky et al., 2014). Taken together, the findings support the effect of genetic variants on differential orienting biases in humans. Here, we propose that this orientating bias can have a link to the directionality bias in visuospatial functions, such as turning or rotation, which is also modulated by differential DA activation levels between the two hemispheres (see below) and possibly co-operate (co-occur) in the same direction.

The functions of DA are mediated by five distinct receptors, namely D1, D2, D3, D4 and D5, in both rodents and humans (Niznik and Van Tol, 1992; Sibley and Monsma, 1992). Among these, D1 and D2 receptors are the most abundant and widely expressed DA receptors which control rotational or motor behaviors (Kobayashi et al., 2004). Animal research has demonstrated interhemispheric anisotropy in DA concentration and its metabolites in the striatal system (Cannon et al., 2009; for a review, see Molochnikov and Cohen, 2014; Schneider et al., 1982) as well as in related structures, such as prefrontal cortex (PFC) and the hippocampus (Fride and Weinstock, 1987; Molochnikov and Cohen, 2014). For example, research in rats has shown that the mean level of D2 binding was 23% greater in the left than the right striatum, while in mesolimbic terminal zones 10% more binding was observed on the right than the left side (Schneider et al., 1982). The DA levels of the orbitofrontal and medial prefrontal subarea in rats are 3–4 times higher than those of a non-prefrontal region of the frontal lobe (Slopsema et al., 1982). The DA levels of the medial prefrontal subarea are also lateralized, the left hemisphere having significantly higher DA level than the right hemisphere (Slopsema et al., 1982). The left hemispheric dominance for DA has been found not only in non-human animal brains, but also in human brains. Studies in humans have shown that the overall DA concentration is greater in the left than the right basal ganglia, particularly in globus pallidus (Glick et al., 1982; Kooistra and Heilman, 1988), caudate nucleus and putamen (Glick et al., 1982). A review study showed that the effects of DA in the basal ganglia are mediated by the nigrostriatal system, extrastriatal dopaminergic projections and intrastriatal dopaminergic neurons (Smith and Kieval, 2000). A couple of reviews also claimed that there is a predominance

of dopaminergic activity in the left hemisphere of human brain (Previc, 1998, 1999, 2007). Like handedness and other types of laterality (Lalan, 2008; Vallortigara et al., 2011), this left-hemispheric dominance for DA might have been evolved through evolution. However, there are a few studies reporting such an advantage in the right side in terms of both D1 (e.g., Nowak, 1989) and D2 (e.g. Drew et al., 1986; Larisch et al., 1998; Nowak, 1989) receptor densities. We suggest that this inconsistency can possibly be accounted for the contextual and cultural factors that can reversely alter the intrinsic DA asymmetry (Yamamoto and Freed, 1984). However, in addition to inter-hemispheric anisotropy, there is evidence that the distribution of DA receptors also varies across the brain structures (within the same hemisphere). The highest concentrations of both D1 and D2 receptors are found in parts of the basal ganglia, particularly in nucleus caudatus, putamen (De Keyser et al., 1988; Palacios et al., 1988; Wamsley et al. 1992), and nucleus accumbens (De Keyser et al., 1988). The medial globus pallidus contains a threefold higher concentration of D1 receptors than the lateral globus pallidus whereas the density of D2 receptors is similar in these two segments (De Keyser et al., 1988). The substantia nigra contained intermediate densities of both D1 and D2 (De Keyser et al., 1988; Palacios et al., 1988), but both are absent in the cerebellum (De Keyser et al., 1988). Both D1 and D2 receptors were also localized in areas outside of the basal ganglia, with low densities of D1 receptors in the neocortex, amygdala and hippocampal formation, and D2 receptors in the hippocampal formation (Palacios et al., 1988).

Based on the above findings we hypothesize that intrahemispheric anisotropy in DA concentration cannot be related to the behavioral laterality or directionality bias in visuospatial functioning (it definitely has some other behavioral impacts, though unknown), and that it is the interhemispheric anisotropy in DA concentration having a direct impact on causing directionality biases in visuospatial functioning. In support of this, the relationship of directionality bias in rats with an asymmetry in DA concentrations between the left and right striata has been evident for both spontaneous (Glick et al., 1980) and amphetamine-induced rotation (Becker et al., 1982; Brass and Glick, 1981; Robinson et al., 1980). Consistently and interestingly, it has been further shown that animals trained to turn in a particular direction exhibited increased DA concentrations in the contralateral caudate while the ipsilateral caudate showed no concentration change (Yamamoto and Freed, 1982; Yamamoto et al., 1982). Studies demonstrated that this tendency was pronounced more in female than male rats (Glick and Ross, 1981; Hines and Gorski, 1985). Some research has identified two categories of rats in both sexes, one category showing turning biases contralateral to the striatum side with a greater amount of DA uptake, and a second category showing turning biases directed towards the same striatum side (Shapiro et al., 1986). The cause of this difference is still unclear and warrants further investigation. A recent review showed that the nigrostriatal system displays symmetrical laterality whereas the mesolimbic system displays asymmetrical laterality; however, the link between DA imbalance and animal behavior is better characterized in the nigrostriatal than in the mesolimbic system (Molochnikov and Cohen, 2014). The DA-mediated lateral bias was observed not only in rodents (Glick and Ross, 1981; Pycock, 1983; Ungerstedt, 1973) but also in higher primates, such as monkeys (Barone et al., 1987; Kori et al., 1995). Though there is no direct evidence from human studies some researchers speculated that turning bias in humans can also be linked to the inter-hemispheric anisotropy in DA concentration (Mead and Hampson, 1996; Mohr et al., 2004) as well. For example, Mead and Hampson (1996) used a behavioral task designed to elicit 160 turns and found rightward turning biases in both the sexes, with a significantly stronger bias in females than males. Backed by the results of other studies they suggested that the underlying basis for this turning bias is possibly an endogenous asymmetry in DA levels between the left and the right striatum (see Bracha et al., 1987b; Glick et al., 1982; Mead and Hampson, 1996). Again, based on the past studies, they suggested that the greater tendency of a rightward turning bias in females was possibly caused by their increased striatal dopaminergic asymmetry which is associated with high endogenous concentrations of ovarian hormones, and magnifies any existing rotational bias (see Becker et al., 1982; Mead and Hampson, 1996; Robinson et al., 1982). One obvious limitation of such an interpretation is that it cannot account for a leftward bias as demonstrated in some other studies (Mohr and Bracha, 2004; Mohr et al., 2003; Toussaint and Fagard, 2008; see above for details). In contrast to a rightward bias, the existence of a leftward bias in some tasks and lack of directionality bias in other tasks suggest that perhaps DA does not equally control the lateralized whole-body movements (Mohr et al., 2004). In the first section of this review, we have shown with considerable body of evidence that our visuospatial perception (e.g., orientation or aesthetic perception) can be biased to the right or clockwise direction, the direction of our turning bias. This suggests that the directional bias or preference in visuospatial perception may also be regulated by the DA system as in the case of turning behavior. This is possible because they typically operate in the same direction. We argue that our turning or rotational behavior can be internally guided by how we see and perceive the objects or stimuli around us, and thus the direction of turning or rotation is perhaps a translated form of the direction of our mental rotation that operates during perceptual processing of the objects or stimuli. However, it remains to be tested whether this is the case by studying the same group of individuals across a variety of perceptual and rotational tasks. Another common and important aspect of our perceptual bias and turning or rotational bias discussed earlier in this review is that the right-handers typically have a greater tendency to exhibit both these biases in a rightward or clockwise direction whereas the left-handers have a tendency to show them in a leftward or anticlockwise direction. This can be interpreted by the difference in hemispheric dominance of dopaminergic processing between the right- and left-handers. A recent PET study in humans has shown that individuals who exhibit rightward orienting bias have higher D2 receptor binding in the left hemisphere and those who exhibit leftward orienting bias have higher D2 receptor binding in the right hemisphere, and that there were strong individual differences (Tomer et al., 2013). Though the study does not give any data about whether this hemispheric asymmetry of D2 receptor binding can be related to handedness and turning or rotational behavior, results of the studies on patients with Parkinson's disease (PD) suggest that perhaps this is the case. For example, recent studies have demonstrated that a significantly larger proportion of the right-handed PD patients have greater motor impairment on their right- than the left-sided limbs (Barrett et al., 2011; Haaxma et al., 2010; Scherfler et al., 2012; Uitti et al., 2005; van der Hoorn et al., 2011, 2012; van Rooden et al., 2009). This has been replicated in a more recent study showing that PD symptoms were dominant on the right side in most of the right-handed patients and on the left side in most of the left-handed patients (Shi et al., 2014). It has been further shown that a significantly greater proportion of the right-handed PD patients had more severely reduced DA transporter binding in the left than the right posterior putamen (Scherfler et al., 2012). In line with this, a very recent study has shown that the right-handed PD patients had predominantly right-sided motor symptoms and left-sided DA defects whereas the effect was opposite in the left-handed PD patients (Kaasinen, 2016). Taken together, the findings suggest that the right-handed healthy humans have a predominance of dopaminergic processing in the left side of the brain and the left-handed healthy humans have such a predominance in the right side of the brain.

Now, let us see how the rightward or clockwise bias in visuospatial functioning can be related to the direction of our attentional bias modulated by DA. As discussed earlier in this review, our focus of attention is predominantly on the left hemifield (as in the case of pseudoneglect for physical stimuli) which perhaps directs our eye movement to the same side. Recent research has shown that humans have a tendency to move their eye to the left on the first saccade when viewing photographs, and that this can be carried-over onto other visuospatial tasks, such as line bisection task (Foulsham et al., 2013; Thompson and Crundall, 2011). However, the leftward bias for focusing attention might also be true for mental attention as it has been shown that the left-right bias occurs not only for physical or visual stimuli but also for mental representations as in the case of bisection of mental number lines and mental alphabet lines (for details, see Section 4). On the other hand, research in both model organisms and normal humans has shown that DA neurotransmission plays a central role not only in locomotion in space (Barron et al., 2010; Pritchard et al., 2007) and orienting or attentional bias (for a review, see Nieoullon, 2002; Tomasi et al., 2009; Tomer et al., 2013; for a review, see Vitay and Hamker, 2007), but also in attention shifting (Vitay and Hamker, 2007). Taken together, we assume that our focus of attention may not be directly on the right, rather it first focuses on the left or top-left and from there it moves away to the right by the activation of DA. In healthy right-handed people, the greater DA concentration in the left hemisphere (see above) increases the likelihood that their focus of attention moves away from the left to the right which in turns creates a turning bias to the right, the side with less DA. This assumption fits well with the theory that the right hemisphere has dominance over the left hemisphere in the left (visual) field spatial attention and spatial processing (Corbetta et al., 1993; Heilman and Van Den Abell, 1979; for a review, see Karim and Kojima, 2010c; Mattingley et al., 1994; Regolin, 2006; Rugani et al., 2010). According to this theory, the deployment of visuospatial attention is controlled by a frontoparietal network in which the posterior parietal cortex (PPC) plays a key role (Duecker et al., 2013; Koch et al., 2013; Szczepanski and Kastner, 2013). A recent fMRI study has demonstrated that the right PPC topographically represents number-space mapping (Harvey et al., 2013) which typically occurs, as discussed earlier, from left-to-right, the direction of rotational or turning bias in most humans (see above). This is very much consistent with a converging neuroimaging evidence that the PPC areas are involved in operating mental rotation during visuospatial representations (for a review, see Zacks, 2008). The PPC is tightly interconnected with the PFC (Katsuki and Constantinidis, 2012; Malhotra et al., 2009). These two dorsolateral areas share many functional properties, exhibiting similar patterns of activation during the execution of cognitive operations, such as working-memory, decision making, and visuospatial attention (Ikkai and Curtis, 2011; Katsuki and Constantinidis, 2012; Malhotra et al., 2009). DA neurotransmission is considered to play a modulatory role of the higher-order processes and neuronal activity in both these cortical areas. It modulates a variety of behavioral and cognitive processes, such as attention and working memory operated in the PFC (for reviews, see Fuster, 2001; Miller and Cohen, 2001), and attention in part by regulating neuronal activity in PPC including precuneus and cingulate gyrus (Tomasi et al., 2009). Consistently, research in monkeys has shown dopaminergic projections from the substantia nigra-ventral tegmental area of the midbrain to the parietal cortex (e.g., Lewis et al., 1988). The local dendritic release of DA by neurons in the substantia nigra pars compacta and ventral tegmental also influences the basal ganglia's functions (Smith and Kieval, 2000), such as motor control (Doya, 2000; Kornhuber, 1978). Thus considering the robust connectivity linking the PFC and PPC, and the role DA plays directly or indirectly in modulating the behavioral, perceptual or cognitive processes and neuronal activity in these areas, we propose that during visuospatial perception the right hemisphere deploys spatial attention to the left visual field where from attention shifts to the right by the activation of DA, creating a left-to-right or clockwise trajectory, and that this may promote a general left-to-right action schema for turning or rotation if demanded.

We further propose that the higher DA concentration (and hence its higher activation) in the left hemisphere may not directly contribute to the rightward turning bias. According to our three-stage model (Fig. 6), some pre-motor or pre-action processes, such as perceptual and cognitive processes, may occur in the brain before we initiate any turning behavior. Thus due to a larger DA concentration/activation in the left hemisphere we have predominant rightward bias in perceiving and forming a spatial map (mental representation) of the world, which as discussed earlier may translate into rightward turning behavior if favored or demanded by the situation. Though data from human studies are still lacking, animal studies lend strong support for this idea. Their accumulating evidence indicates that brain lateralization may have appeared early in evolution (Duboc et al., 2015; Lalan, 2008; MacNeilage et al., 2009; Rogers and Vallortigara, 2015; Vallortigara et al., 2011) and may have first evolved for perceptual processes (Rogers, 2002; Rogers and Andrew, 2002; Vallortigara, 2000; Vallortigara and Rogers, 2005). Laterality has been found in species as remote as birds, amphibians, reptiles, fishes and arthropods (for reviews see Bisazza et al., 1998; Rogers and Andrew, 2002; Vallortigara and Rogers, 2005). Evidence of brain lateralization in low vertebrates mainly focuses on perceptual functions (Vallortigara, 2000), suggesting that hemispheric specialization may have evolved first for perception. Then lateralization for motor functions, which has evolved later, may have been influenced by the preexisting perceptual anisotropies (Chapelain and Blois-Heulin, 2009). This seems to contradict the innate rightward head turning bias in humans (see above). However, this contradiction does not necessarily preclude the role of perceptual lateralization in motor behavior and vice versa. As explained previously in this review, even if motor lateralization, such as head turning bias may have been evolved first, this may not directly translate into rightward turning or rotational bias in adulthood. Rather, there are perhaps some intermediate processes, enhanced by the innate head turning bias to the right, such as perception and cognition that facilitate the successful translation of the innate head turning bias into an adulthood turning or rotational bias. Here we propose that an increased DA level and activation in the left hemisphere (Glick et al., 1982; Kooistra and Heilman, 1988; Previc, 2007) may facilitate detailed and precise mental representation of the objects/stimuli at rightward/clockwise orientation. The mental representation with a preferred directionality as with the clockwise direction may be more stable or easily achieved than representation with the opposite directionality as with anticlockwise direction. This may enhance perception, learning and memory of the clockwise oriented rather than anticlockwise oriented objects and spatial regions. Perhaps this is why customers remember more products in a store with clockwise layout than with an anticlockwise layout (Groeppel-Klein and Bartmann, 2008, 2009; for details, see Section 5).

The above discussion clearly demonstrates the role dopaminergic neurons play in producing a rightward or clockwise bias in cognitive and motor behaviors in both animals and humans. However, as the number of dopaminergic neurons is few in the cerebral cortex (Chinta and Andersen, 2005) perhaps they are not the candidate solely responsible for this bias. Other specialized cortical neurons might also be recruited in the process. The clockwise and anticlockwise biases in a wide range of visuospatial perceptions and turning behaviors led us to speculate that the cortical neurons which modulate these behaviors function in a direction

specific fashion; in majority of the population cortical neurons prefer a clockwise direction and simultaneously produce a greater response to the clockwise oriented objects/stimuli while other neurons prefer an anticlockwise direction and simultaneously produce a greater response to the anticlockwise oriented objects or stimuli. Whether and how much an individual will exhibit a clockwise bias or an anticlockwise bias depends on the differences in strength between the competing neuron subpopulations the individual has in the brain, the strength of a neuron subpopulation being determined by the number of neurons forming that subpopulation and perhaps the relative strength of firing as in a biased competition framework (Desimone and Duncan, 1995). The question is where in the brain lie these subpopulations of neurons? It is a difficult question that cannot be answered precisely without a scientific enquiry. However, let us look into the existing literature to find out some plausible answer. Previous studies have identified the direction-specific functions of cortical neurons. Specifically, it has been demonstrated that V1 (striate cortex) comprises neurons that are specific not only to the stimulus orientation, but also to the local motion direction (Pasternak et al., 1985; Reid et al., 1991), whereas MT (middle temporal) neurons to which V1 neurons dispatch the local motion signal via the extrastriate V2 and V3 (Albright, 1984; Britten et al., 1992) are specialized for encoding the direction of motion (Albright et al., 1984; for a review, see Born and Bradley, 2005; Diogo et al., 2003; Malonek et al., 1994; Maunsell and Van Essen, 1983a; Zeki, 1974). Neurons of these two cortical areas that are highly sensitive to a particular motion direction do not respond or respond very weakly to the stimuli of an opposite motion direction. However, MT neurons are tuned to unidirectional local motions (for a review, see Born and Bradley, 2005) and have little sensitivity to a global flow structure (Smith et al., 2006). Area MT lies in the posterior bank of the superior temporal sulcus (STS) and projects to the immediately adjacent area MST (medial superior temporal area) lying in the anterior bank of STS (Andersen, 1989; Desimone and Ungerleider, 1986; Maunsell and van Essen 1983b). Unlike MT which is weakly activated by stimuli confined to the ipsilateral hemifield, MST is strongly driven by ipsilateral stimuli (Dukelow et al., 2001; Smith et al., 2006). Area MT encodes the basic elements of motion whereas MST has the capacity of higher-order motion-processing, such as global motion in optic flow (for a review, see Britten, 2008; Duffy and Wurtz, 1991; Wall et al., 2008), and has been implicated in the perception of both object and self-motion (Britten and Van Wezel, 1998; Tanaka et al., 1993). Area MST is typically divided into a lateral (MSTl) and a dorsal (MSTd) subregion. Like neurons in V1 or MT, neurons in MSTl are directionally selective and respond to translating bars or dots (Albright, 1984; Hubel and Wiesel, 1962; Livingstone and Hubel, 1988; Maunsell and Van Essen, 1983a,b). However, it is MSTd that has neurons with large receptive fields which respond to large field stimuli or objects (Graziano et al., 1994). While some neurons in this portion respond to simple translational motion, many others respond to clockwise or anticlockwise rotation, and some others respond to expansion or contraction (Duffy and Wurtz, 1991; Graziano et al., 1994; Saito et al., 1986; Smith et al., 2006; Tanaka and Saito, 1989; Wall et al., 2008). These motions are generated as a result of an observer's own movement through the environment (Graziano et al., 1994; Wurtz, 1998). However, area MST demonstrates a projection to area 7a and LIP (lateral intraparietal area) of PPC (Maunsell and Van Essen 1983b; Seltzer and Pandya, 1984). Research has shown that areas 7a and LIP are involved to integrate visual, somatosensory, auditory and vestibular signals, whereas area MSTd integrates visual motion signals, similar to those generated during an observer's movement through the environment, with eye-movement and vestibular signals (for a review, see Andersen, 1997). The spatial representations in area 7a and LIP appear to be important for specifying the locations of targets for actions such as eye movements or reaching whereas the spatial representation in area MSTd is important for navigation and the perceptual stability of motion signals (for a review, see Andersen, 1997). Thus the three PPC areas are involved in spatial perception as well as visually guided motor control. In relation to this, we have seen somewhere in this section that DA modulates visuospatial attention and turning or rotational behavior at least in part by regulating neuronal activity in PPC. Thus, taken together, we propose that there may be subpopulations of neurons in MST or in some other areas of PPC specialized to determine the direction in which a person or animal prefers to perceive, think and behave, such as turn or rotate, in a particular environment or stimulus situation.

The direction specific neurons possibly form and develop during the early stages of prenatal development which cause human fetuses, as mentioned earlier, to turn their heads to the right rather than to the left at an age for moving the head freely (Konishi et al., 1986; Ververs et al., 1994). This prenatal head turning bias promotes visual orientation to the right side (Coryell and Michel, 1978; Konishi et al., 1987) subsequently after birth, and is maintained more or less throughout the lifespan, perhaps depending on how much they are shaped by the cultural or environmental factors due to neural plasticity (Fig. 7). Turkewitz and Creighton (1974) argued that once an infant turns its head, for whatever reason, to the right, the right biased posture differentially affects sensory thresholds, in such a way as to facilitate subsequent turning to the right. They further proposed that an innate neural asymmetry in the programming of movement accounts for the first manifestation of a rightward bias, and its maintenance throughout the lifespan. We agree with this idea of an innate neural asymmetry, but not with their view that the innate head turning bias to the right directly translates into a whole body turning. As mentioned above, we believe that this translation is obvious and indirect rather than direct; that is, some perceptual and cognitive operations (which are also biased to the same direction) are necessary before making a decision of turning to the preferred direction (for details, see three-stage model in Fig. 6). We also propose this innate neural asymmetry is such that the specialized MST neurons (or other types) might overrepresent the clockwise orientation in right-handers and anticlockwise orientation in left-handers. Thus the combined effect of neural populations typically favors to perceive and turn clockwise in the right-handers and anticlockwise in the left-handers. However, further empirical research in careful controlled situation is warranted to examine whether cortical neurons are organized in this fashion or have this kind of property per se.

9. Culture as an indirect modulator of perceptual-motor bias in humans

As discussed earlier in this review, there has been no full consensus so far on the mechanisms underpinning perceptual-motor biases. However, based on the findings reviewed here it appears that there are probably two major turner groups: clockwise versus anticlockwise turners. The key predictors that appeared in the literature to explain this asymmetry are different kinds of brain laterality, such as handedness, DA imbalance etc. However, the directionality of this asymmetry may not be always stable and consistent at the population level. It has been shown that in addition to this between-group asymmetry, there are also some in-group discrepancies in experimental results, that is, right-handers or left-handers did not always show the bias consistently in the same direction (see Sections 1 and 5), suggesting that the relationship of the directionality biases to handedness is not always straightforward. The lack of this straightforward association is perhaps primarily caused by the complex genetic architecture of handed-

ness (Rockman, 2012; Mackay, 2014; for a review, see Versace and Vallortigara, 2015). However, the in-group discrepancies can further be accelerated due to the lack of control of the factors (e.g., time) likely to modulate this bias, or due to other methodological differences, such as differences in experimental task, sensory deprivation or reliable sensory signals as in the case of studies on veering behavior discussed earlier. The between group asymmetries (left-handers vs right-handers) can further be shaped or modified by environmental/cultural transmission (see Section 7) which occurs through learning from parents, elders, previous generation, or conforming to the majority view (Lalan, 2008). The environmental/cultural fluctuations may have a *phasic* modulating effect on the manifestation of the directionality bias for discrete circumstances (Liederman and Kinsbourne, 1980b). As we have seen in this review, the directionality bias in visuospatial perception and turning behavior is related to handedness and learning factors. These two factors may vary across cultures; in some cultures left-handedness is discouraged (e.g., Asian cultures, Muslim cultures; Fagard and Dahmen, 2004; Hoosain, 1990; Payne, 1987; Singh and Kundu, 1994) while in other cultures it goes unnoticed (Western cultures; Fagard and Dahmen, 2004); in some countries people are expected to walk and drive on the right side of roads (e.g., USA) while in other countries it is on the left side (e.g., Japan); again in some cultures people read and write from left to right (e.g., Western countries) while in other cultures people read and write from right to left (e.g., Arabian countries, Japan). Thus the discrepancy in experimental results might reflect division of the whole population into a few groups: some people are bias to the clockwise direction, some to the anticlockwise direction while others remain unbiased, unreliably biased or mildly biased. The extent of this bias depends on the interaction of the neurogenetic/neurobiological factors with the environmental/cultural factors we are exposed to (Fig. 7). We propose that the mental representation which is predominantly biased to the clockwise direction may be enhanced or in some cases altered and modified by the influences of environmental/cultural factors, such as scanning habits (reading and writing direction) and traffic rules. Research has shown that the neurobiological and cultural factors modulate the directionality bias (e.g., in drawing, visual aesthetic preference) in both the left- and right-handers; however, left-handers are more influenced by environmental/cultural factors than are right-handers (De Agostini et al., 2010; Dreman, 1974, 1977; Shanon, 1979). One of these studies further claimed that the development of left-to-right (i.e., clockwise) trend in directionality bias (in drawing) in right-handers is natural as they exhibit this sort of bias prior to reading education (Dreman, 1974). We argue that this so called naturally developed directionality bias might have been achieved, intensified or modified through cultural evolution or training. As the world (e.g., written text, letters in text, reading and writing direction, cultural expectation) mostly favors clockwise (rightward) direction, most of us have clockwise bias in both visuospatial perception and turning behaviors. Here the question is how cultural perspective influences laterality issues, such as dopaminergic asymmetry between the hemispheres or brain structures. This is a difficult question that cannot be answered directly with the current knowledge we have. However, studies in animal models have shown that practice increases individual and population laterality in a variety of tasks (Castellano et al., 1987, 1989), and that animals trained to turn in a particular direction exhibit significantly increased DA concentrations in the contralateral hemisphere (Yamamoto and Freed, 1982, 1984; Yamamoto et al., 1982). Though interhemispheric DA imbalance is an inherent brain property, it is not resistant to behavioral modification; rather it can be changed or even altered reversely through training (Yamamoto and Freed, 1984). Thus, if practice increases behavioral laterality and training in a particular direction can increase DA concentration in the contralateral hemisphere in animal models, we speculate that culture can also play a role in similar fashion to change DA concentrations in human brain. Previc (1991) has commented precisely that culture plays a role not only in the establishment of language and motoric lateralization (e.g., handedness), but may also well contribute to any neurochemical lateralization. In fact, DA concentration is associated with handedness – presumably the left-handers have greater dopaminergic content in the right hemisphere and the right-handers have greater dopaminergic content in the left hemisphere (de la Fuente-Fernández et al., 2000; Mohr et al., 2003; Previc, 1991, 1996). Thus culture can possibly change DA concentration and hence DA activation by forcing overtly or covertly, for example, to behave as right-handers (see above). However, careful controlled observations are warranted to test this assumption.

10. Future research directions

Reviewing the relevant literature of non-human animal and human studies we have shown here a close connection between cerebral dominance and various expressions of behavioral lateralization, such as the diversity of directionality biases in visuospatial perception and turning behavior. Based on the relevant literature, we have inferred that behavioral lateralization, such as clockwise or anticlockwise biases in such visuospatial functioning, develops in response to the interactions between neurogenetic/neurobiological factors and environmental/cultural factors. Research in the past few decades has focused on the relationship of the lateral bias in turning behavior with the asymmetry in DA concentration in the brain and the preferential handedness. The role of DA in fostering clockwise or rightward turning behavior has been well established, in both animal and human studies. However, it is still unknown whether DA has a similar and direct role in causing directionality biases in visuospatial perception. Furthermore, the clockwise biases in visuospatial perception have been claimed here based on the experiments carried out mostly in two cardinal orientations and rarely in oblique and other tilted orientations. Research in other diverse orientations should be designed to confirm the findings so far obtained, and also to assess further the asymmetrical DA activity in the brain. More importantly, how the left and right hemispheres interact in performing visuospatial tasks in a particular orientation (clockwise or anticlockwise) has not yet been fully understood. Future studies should therefore be designed to address this issue in a more rigorous manner. Studies can further attempt to investigate whether there are subpopulations of cortical neurons for processing the clockwise and anticlockwise oriented objects/stimuli, and whether the clockwise neurons (if any) are overrepresented in the right-handers' brain and anticlockwise neurons in the left-handers' brain. Studies should also be designed to investigate simultaneously the directionality bias in both visuospatial perception and turning behavior (using the same group of participants), and this will lead to the establishment of a clear link (if any) between the directionality bias in visuospatial perception and that in turning behavior. We further suggest that studies can be designed to examine whether the clockwise or anticlockwise bias also exists in basic and aesthetic tactile perception, such as in the aesthetic appreciation of tactile arts or objects. For example, it would be of interest to study left-to-right or a right-to-left orientation or directionality cues, as in the case of visual arts or objects. All these studies can be designed to assess the role of visual experience by including fully sighted and visually impaired (low vision) people and some by including totally blind people (e.g., tactile perception, turning or rotational behavior). Thus we will be able to understand whether people who are clockwise turners have perceptual (e.g., aesthetic) preferences different from those who are anticlockwise turners.

11. Concluding remarks

Based on a detailed analysis of the empirical findings in visual psychophysics and visual neuroscience we proposed here a three-stage model of directionality bias in visuospatial functioning as well as a dynamic model of the origins of such biases. The *Perception-Action-Laterality* model asserts that the directionality bias reflects a bias in mental representation, and possibly first occurs at a covert behavioral level, such as in perception and cognition, and may translate later into overt behaviors, such as turning or rotational behaviors. This focused review shows overwhelmingly that a majority of the population exhibits such a bias to the clockwise direction in both simple and complex, and both covert and overt, visuospatial functions. The most appealing aspect of this dynamic spatial-mapping model is that it can explain asymmetry in visuospatial functions across the stimulus orientations, and across a wide range of visuospatial stimuli or phenomena, including perception, cognition, and motor behavior, ranging from very basic visuospatial or attentional processes up to rather complex, culturally-bound behaviors, such as artistic production or art appreciation.

The model of the origins of biases posits that the biases in visuospatial functioning are precursors to cerebral lateralization indexed by handedness, eye dominance, and asymmetrical DA level and probably to an innate neurogenetic asymmetry. These neurobiological factors lay the foundation for functional biases which is reorganized and shaped by the cultural or environmental factors in a dynamic biased competition framework. As this bias can be altered or modified by experience and learning due to the plasticity property of cortical networks, there are always some individuals who exhibit the bias in a reversed direction; or in some cases the bias is seemingly absent. Thus the most striking feature of this dynamic model is that it can explain not only the two major categories of biases in terms of direction and strength, but also the unbiased, unreliably biased or mildly biased cases in visuosptial functioning. The time is ripe for future research to investigate if the clockwise or anticlockwise bias does also occur in tactile perception, and if there is any real association between perceptual orientation (in both visual and tactile domains) and turning or rotational orientation, and whether they share some behavioral and neural mechanisms.

In conclusion, most of the evidence available to date in the literature favors perceptual-motor biases in a clockwise direction in a situation where external factors are unlikely to block the spontaneous behavior. Surprisingly, many sporting facilities are solely designed for turning, running or racing in an anticlockwise direction, but not based on any empirical evidence of convenience for the players. The ideas proposed here might have practical implications for the design of public spaces, such as sports facilities, schools/colleges, store displays, museums, business centers, and also for the design and presentation of products on the shelves in an appealing fashion or to best enhance human performance (Proulx et al., 2016).

Conflict of interest

Authors declare that they have no potential conflict of interest.

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